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The Response of Understory Vegetation to Major Canopy Disturbance in the Subalpine Forests of Colorado

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THE RESPONSE OF UNDERSTORY VEGETATION TO MAJOR CANOPY DISTURBANCE IN THE SUBALPINE FORESTS OF COLORADO

by

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Thesis directed by Professor Thomas T. Veblen

The importance of natural disturbance in plant community dynamics has long been recognized, but only recently has it been treated as a fundamental process in many ecosystems. Disturbances vary in space and time and often change the structure and composition of communities, resulting in patchiness within the landscape. Diversity may be enhanced by disturbances occurring at particular frequencies and intensities. The purpose of this research was to quantitatively examine the response of understory vegetation to major canopy disturbance of two types: blowdown and insect attack. In particular, changes in structure and diversity were investigated.

Understory vegetation was sampled in ten stands with varying severities of canopy disturbance in subalpine forests in Colorado. Percent cover of all vascular plant species was estimated, from this mean cover and richness were calculated. Size and species of live and dead trees, logs, and stumps were recorded, and densities of tree seedlings and saplings were sampled. Hemispherical photographs allowed estimation of diffuse light. Non-parametric correlations were used to test

relationships between understory and canopy characteristics.

The results indicate that moisture conditions control the broad patterns of understory structure and composition, but richness and cover both tended to be higher in the more severely disturbed patches than in the old-growth patches. Also, it appears that shrub richness and forb richness respond differently to tree mortality. The release of soil nutrients and moisture may be more important to herbaceous species than shrubs, which appear to respond more to the release of light.

It appears that the more severely disturbed patches favor increased tree regeneration. Seedling and sapling densities show an apparent increase in patches with increased tree mortality. In more mesic patches, spruce seedlings show high percentages of establishment on decaying logs.

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CONTENTS

TABLES

Table

FIGURES

Figure

CHAPTER I

INTRODUCTION

Disturbance and Patch Dynamics

Although the importance of natural disturbance in plant community dynamics has long been recognized (Pickett and White 1985), disturbance has traditionally been seen as a resetting of successional trends. According to this view, following large-scale disturbance the physical and biotic parameters of a disturbed site eventually return to their original climax or equilibrium states (Clements 1916, Tansley 1935). The traditional view of succession has not encouraged recognition of the importance of repeated disturbances in affecting the structure of plant communities and landscapes. However, recent workers in the fields of ecology, forestry, and geography have begun to treat disturbance as a fundamental process in many ecosystems (see reviews by Grubb 1977, Miles 1979, White 1979, Vale and Parker 1980, Pickett 1980). In this context, disturbance refers to "...any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources,

substrate availability, or the physical environment" (White and Pickett 1985). Disturbances vary in space and time. The importance of quantitatively describing disturbance regimes, or the spatial and temporal characteristics of the disturbances of a particular area, is widely recognized (Pickett and White 1985).

Discrete events, such as forest fires or blowdowns, often change the structure and composition of communities, resulting in patchiness within the landscape. The most important characteristics of patches include: 1) the pattern of patch creation in time and space; 2) patch size and structure; and 3) the changes within individual patches of community structure and composition due to species availabilities, adaptations and interactions (Thompson 1977, 1978, Pickett and Thompson 1978). A patch dynamic view of plant community structure emphasizes the importance of repeated disturbances and the growth or establishment opportunities created for some species (Pickett 1980, Veblen in press).

Much discussion has focused on how disturbances affect species diversity and coexistence (e.g. Loucks 1970, Connell 1978, Denslow 1980b, 1985). In general, these authors propose that species diversity is maintained by the occurrence of disturbances at particular frequencies or intensities. Connell's (1978)

"intermediate disturbance hypothesis" suggests that as the interval between disturbances increases, diversity also increases. This is due to the increased time available for species to disperse and grow into disturbed patches. But as the disturbance interval becomes even longer, competitive processes become more important and elimination of the less competitive species may occur (Loucks 1970, Connell 1978, Denslow 1985). Thus, factors preventing competitive equilibrium within plant communities may allow nonequilibrium coexistence of species (Pickett 1980). Disturbances might also enhance diversity by increasing environmental heterogeneity, thereby adding opportunities for specialization and resource partitioning (Grubb 1977, Denslow 1980a, Auerbach and Shmida 1987, Rebertus et al. 1989).

Most studies of disturbance in forested habitats have emphasized tree population responses (e.g. Heinselman 1973, Oliver 1981, Woods and Whittaker 1981, Romme and Knight 1981, Runkle 1982, Canham and Loucks 1984, Veblen 1985) or the inhibition of tree regeneration by the forest understory (Ehrenfeld 1980, Maguire and Forman 1982, Veblen 1982, Brokaw 1983). Much less work has been done on the patch dynamics of understory vegetation. Most studies of understory response to disturbance have examined responses to

canopy gaps in mesic deciduous forests (Thompson 1980, Huenneke 1983, Moore and Vankat 1986) or mixed deciduous-evergreen forests (Runkle 1982, Cook and Lyons 1983, Veblen et al. 1977, 1979). Coniferous forest understories have received less attention, except in relation to stand recovery following fire (e.g. Peet 1981, Armour 1984), or understory response to canopy gaps caused by treefalls or thinning by logging (Alaback 1982, Alaback and Herman 1988, Stewart 1988). Little research has been done on understory responses to large-scale canopy disturbances in coniferous forests. There is a need for quantitative information on the response of forest understory vegetation to major canopy disturbance in the coniferous forests of western North America.

This study examines the response of understory vegetation to two forms of large-scale canopy disturbance in subalpine forests of the southern Rocky Mountains: massive blowdown and spruce bark beetle (Dendroctonus rufipennus) outbreaks.

Objectives

The objective of this research was to quantitatively describe responses of understory vegetation to recent major canopy disturbances by insects and large blowdowns in representative subalpine

forests in Colorado. The canopy openings created by these disturbances vary in size and extent in a stand, creating patchiness in soil resources and light levels. Corresponding changes in understory structure and composition can be expected. I sought to answer the following questions: how is species richness related to the severity of the disturbance? Is understory composition related to changing canopy composition following disturbance? Does the understory structure and composition differ under more severely disturbed canopies from that under less disturbed canopies?

Specifically, I hypothesized that the release of light and soil resources due to the death of canopy trees would result in: 1) an increase in percent cover of the understory; 2) a change in relative importance of shrub versus herbaceous species; 3) an increase in tree seedling numbers; and 4) an increase in species diversity.

CHAPTER II

LITERATURE REVIEW

Forest Understory Vegetation

Understory Response to Canopy Composition

The structure and composition of forest understory vegetation is influenced by patterns of resource heterogeneity under the forest canopy (Bratton 1976, Hicks 1980, Spurr and Barnes 1980, Beatty 1984). Understory plants must compete with the dominant tree species for light, water and soil nutrients. Their ability to compete is affected by: the composition and structure of the canopy; whether the canopy is evergreen, deciduous or mixed; seasonal changes in solar radiation; the presence of rocks and fallen trees on the forest floor; and gradients of nutrients in the soil. In general, more solar radiation reaches the forest understory as direct light in coniferous forests while deciduous forest understories receive more diffuse light (Anderson 1966, Chazdon 1988). Both light intensity and throughfall precipitation in coniferous forests increase with a decrease in average canopy cover. This correlates with an increase in herbaceous cover

(Anderson et.al. 1969).

Variation in canopy composition and structure can greatly influence the abundance and size of understory species. For example, in mixed broadleaved evergreen-deciduous Nothofagus forests near timberline in south-central Chile, Veblen et al. (1977, 1979) demonstrated that the bamboo Chusquea tenuiflora is more abundant and taller beneath evergreen trees where spring snow-melt is earlier and summer light levels are greater. This results in a longer vegetative period which favors Chusquea (Veblen et al. 1977, 1979).

Canopy composition also strongly influences soil characteristics and therefore the distribution of understory species. The presence of hemlock (Tsuga canadensis) in a beech-maple forest in eastern New York was accompanied by different soil properties from those found in non-hemlock areas (Beatty 1984). Forest areas with hemlock had greater soil organic matter content, greater available nitrogen and litter depth, lower soil moisture content and pH, and no frost heaving. As a result of these properties, forest areas with hemlock had homogeneous patterns of understory distribution. Treefall pits and mounds lacked characteristic species assemblages. Non-hemlock patches of forest did have unique species assemblages associated with pits and mounds. Zinke (1962) demonstrated that soil properties

under Pinus contorta trees were influenced by the leaf and bark litter characteristics under individual trees. Moir (1966) reported suppression of herbaceous growth beneath ponderosa pine (Pinus ponderosa) canopies in Washington by heavy litterfall from the trees. The thick O horizons were subject to extreme drying during the summer months. Crozier and Boerner (1984) showed that stemflow-induced soil nutrient gradients may be important in maintaining spatial heterogeneity and thereby understory species diversity. Variation in understory composition under Quercus alba trees was closely correlated with differing concentrations of calcium, sulfate and hydrogen ions in Q. alba stemflow.

Understory Response to Microtopographic Gradients

Microtopography (e.g. rocks, fallen logs, or pits and mounds from the uprooting of trees) influences soil temperature, moisture, and nutrients (Bratton 1976, Thompson 1980, Putz 1983, Beatty 1984). This in turn affects the distribution and abundance of understory plants. Microtopographic gradients within a species-rich cove hardwood forest result in a patchy distribution of forest herbs (Bratton 1976). Phacelia fimbriata was uncommon near the base of large trees and increased in abundance with distance from the trunk. In contrast, several other species were most abundant at

the bases of trees and next to rocks or on fallen logs (Bratton 1976). The differences in species distributions were related to variations in soil moisture, soil nutrients and litter depth. Beatty (1984) found that treefall mounds were drier, poorer in nutrient content, had less organic matter, less litter cover and less snow accumulation, than pits. The mounds were also more subject to frost heaving. As a result of these differences, pits and mounds each had characteristic species assemblages. Putz (1983) also found distinct understory species assemblages specializing on pits, rootthrow mounds and fallen logs of treefalls.

Understory Response to Canopy Disturbance

Disturbances are common in forest communities and affect the resources available to understory plants (Heinselmann 1970, White 1979, Pickett and White 1985). The deaths of dominant trees permit the increased growth of already established individuals or create openings for the establishment and growth of new individuals (Marks 1974, Ehrenfeld 1980). Canopy disturbances change resource availability for understory plants by: 1) increasing light, water and soil nutrients due to reduced uptake by trees injured or killed; and 2) changing soil nutrients by decomposition of organic

matter or disruption of nutrient cycling (Canham and Marks 1985).

Gaps can directly affect herb, shrub and tree regeneration patterns and result in shifts in the composition and structure of vegetation. Brokaw (1982) defines gaps as openings in the forest canopy greater than about 5 m across. These openings increase light levels on the forest floor (Geiger 1965, Chazdon and Fetcher 1984) and can result in air and soil temperature regimes very different from those found under closed canopies (Collins et al. 1985, Moore and Vankat 1986, Chazdon 1988).

Ehrenfeld (1980) investigated understory responses to single and multiple-tree gaps in an oak forest defoliated by gypsy moths. She found that gaps favored woody understory species. Furthermore, the density of young individuals of the canopy species tended to be inversely related to understory density. Huenneke (1983) noted that single-tree gaps caused by the death of Ulmus americana had an understory composed of seedlings and saplings of the dominant canopy species, as well as understory shrubs typical of closed-canopy mixed-deciduous hardwood forests. Multiple-tree gaps, however, had understory shrubs not commonly found beneath a closed canopy. Huenneke (1983) also found that a dense shrub cover in larger gaps impeded the

regeneration of canopy species. Veblen et al. (1977, 1979) found similar results in the temperate forests of Chile, where a dense understory of bamboo (Chusquea tenuiflora) completely prevents the regeneration of both Nothofagus betuloides and N. pumilio. Regeneration of Nothofagus in these near-timberline forests must therefore occur following the synchronous flowering and subsequent mass death of the bamboo. Catastrophic disturbance which partially or totally eliminates bamboo from the understory also permits Nothofagus regeneration (Veblen and Ashton 1978, Veblen et al. 1979).

Herbaceous understory diversity and cover may respond in a variety of ways to canopy gaps (see Collins et al. 1985). Brewer (1980) concluded that dense regeneration of sugar maples (Acer saccharum) in treefall gaps lead to a decline in herb layer diversity in climax beech-maple forests. After a half-century of stand development only spring ephemerals appeared to be maintaining their abundance. Davison and Forman (1982) found that herbaceous cover increased with gap formation, but that herb richness decreased. Moore and Vankat (1986) found that herb species richness in a beech-maple forest was largely unaffected by gap dynamics, even though herb cover increased after gap formation and then decreased following canopy closure.

Understory successional changes in temperate,

coniferous forests following fire, logging, and/or windthrow have been described by Ahlgren (1960), Alaback (1982), Zamora (1982) and Alaback and Herman (1988). These workers have found that initially herbs, then shrubs dominate these stands. These stages are followed by canopy closure by rapidly growing trees and the inhibition of understory growth. Alaback (1982) found that after 150 to 200 years there was an understory reinitiation stage, whereby mortality of the post-disturbance cohort of trees allowed renewed growth of shrubs.

Stewart (1988) investigated relationships between canopy type, disturbance history, and understory composition in conifer forests of the Cascade Range, Oregon. He found that understory richness was greater in gaps of all canopy types compared to closed forests. Disturbance history (fire or treefalls) influenced canopy composition (Stewart 1986, 1988) and the prevalence of canopy openings. This finding suggests that the understories of these stands also reflect stand disturbance history.

Subalpine Coniferous Forests of the Southern Rocky Mountains

Disturbance Regimes and Stand Dynamics

The montane and subalpine forests of the Rocky Mountains have been characterized as "disturbance phenomena" (Peet 1981, 1988). Forests commonly are in some stage of recovery following disturbance by fire, insect attack, wind, avalanches or logging (Peet 1981, Veblen and Lorenz 1986). These disturbances create mosaics of stands of varying structure and composition (Peet 1988). Fire has historically been considered the most important disturbance agent, but windstorms are frequent and can cause extensive blowdowns (Peet 1981, Alexander 1987, Veblen et al. 1989a).

Fire. The importance of wildfire as a stand-initiating disturbance in the subalpine forests of the southern Rockies has been well documented (Clements 1910, Whipple and Dix 1979, Romme and Knight 1981, Romme 1982, Peet 1981, Veblen 1986a). The patterns of replacement of the seral tree species, lodgepole pine (Pinus contorta Dougl. var. latifolia Engelm.) and quaking aspen (Populus tremuloides Michx.), by subalpine fir (Abies lasiocarpa [Hook.] Nutt.) and Engelmann spruce (Picea engelmannii [Parry] Engelm.), are strongly affected by moisture and elevation gradients and by seed

availability (Peet 1988).

Moderately xeric sites are the most common sites in the subalpine zone of the southern Rockies. Lodgepole pine is the primary colonizer following fire on such sites, although spruce and fir may be present in varying numbers. However, fir generally does not begin to establish in large numbers until several decades after stand initiation (Whipple and Dix 1979, Peet 1981, Veblen 1986b). Eventually, spruce and fir replace lodgepole pine as the canopy dominants. Spruce will tend to dominate in more mesic stands, while fir will do so in drier stands (Peet 1981).

On mesic, favorable sites, spruce dominates the post-fire stand initiation phase because it can establish more successfully on bare mineral soil than fir (Knapp and Smith 1982, Peet 1988). Establishment and growth are usually rapid, leading to dense stands that inhibit further seedling establishment (Peet 1981). In mature or old-growth spruce-fir stands, individual tree mortality and subsequent treefalls permit renewed regeneration (Peet 1981, Veblen 1986a). Generally, fewer spruce will establish than fir, because the latter establishes better under low light levels and on thick litter layers (Knapp and Smith 1982). However, the greater abundance of fir regeneration in old-growth stands is compensated for by the greater longevity of

spruce, permitting these species to coexist (Oosting and Reed 1952, Veblen 1986b).

Insect pests. Spruce bark beetle outbreaks (Dendroctonus rufipennus [Kirby]) in the mid-1800s killed up to 40% of the mature Engelmann spruce on Grand Mesa, Colorado. Infestations in the 1940s decimated spruce stands in the White River National Forest, Colorado (Schmid and Hinds 1974, Schmid and Frye 1977). Outbreaks generally follow blowdown or logging operations which leave piles of slash (Schmid and Frye 1977). Spruce beetles preferentially attack large-diameter trees and leave trees < 10 to 15 cm dbh untouched (Schmid and Frye 1977).

The effects of such outbreaks on stand structure and development have received little attention. Miller (1964, 1970) examined age structures (largely inferred from size structures) of two spruce-fir stands on the White River Plateau of northwestern Colorado that had suffered a severe spruce beetle outbreak during the 1940s. He suggested that irregular age structures indicated earlier outbreaks. Schmid and Hinds (1974), and Veblen et al. (1989b) have shown that spruce beetle outbreaks result in increased tree seedling establishment and accelerated growth rates of surviving host and non-host species.

Windthrow. Damaging windstorms and blowdown are common in the southern Rockies (Hansen et al. 1978, Glidden 1981, Alexander 1987, Veblen et al. 1989a). However, little work has been done on stand dynamics subsequent to blowdown.

After a 15-ha blowdown in a xeric subalpine lodgepole pine stand, Veblen et al. (1989a) found a dramatic growth release among subcanopy Engelmann spruce and subalpine fir, rather than new seedling establishment. Thus, successional replacement of lodgepole pine by spruce and fir was accelerated by the blowdown. This is in contrast to the new establishment response of pine and spruce following wildfire in similar subalpine stands (Peet 1981).

Subalpine Forest Understory Vegetation

The vegetation of subalpine Picea-Abies forests is remarkably consistent throughout the Rocky Mountains (Peet 1988). There is a latitudinal pattern of increasing diversity at higher latitudes (Peet 1988). In open, dry stands, a continuous cover of Vaccinium dominates (e.g. Vaccinium scoparium Leiberg, V. myrtillus L.). Few herbaceous species are present, the more widespread being Arnica cordifolia Hook., Orthilia secunda L., and Polemonium delicatum Rydb. On moist sites, a lush herbaceous layer is common, including such

genera as Calamagrostis, Carex, Erigeron, Mertensia, Mitella, Saxifraga, and Senecio. Shrub genera that may also be present include Linnaea, Lonicera, Paxistima, and Viburnum).

Little detailed work has been done to document the patterns of understory structure and composition in these forests. Ecophysiological studies by Young and Smith (1979, 1980, 1982 and 1983) in Wyoming subalpine forests have demonstrated the importance of sunfleck activity and cloud cover for several understory species. Knight et al. (1977) showed that small-scale patchiness in the distribution of understory vegetation is related to snow banks that persist until early July. Cover of Carex geyeri and V. scoparium was noticeably lower where snow persisted until mid-summer.

Patterns of understory species diversity in the Rockies are related to elevation, site moisture conditions, and successional development (Peet 1978, 1988). In high elevation forests near timberline, the forests with highest richness occur on wet, boggy sites with relatively low tree cover. Richness decreases on more xeric sites. At middle elevations (ca. 2900 to 3100 m) richness is lowest near the center of a moisture gradient, and highest near the moist end of the gradient (Peet 1978). Sites with the lowest diversity shift progressively toward the mesic end of the moisture

gradient with decreasing elevation (Peet 1978).

Successional development following fire on more favorable sites is initially rapid and canopy closure results in competitive inhibition of understory growth (Peet 1978, 1981). As stands age, natural thinning and gaps allow increased diversity and growth of the understory. On unfavorable sites (xeric or high elevation), recovery from stand disturbance is slow and canopy development may never inhibit understory growth. Again, Peet (1978) emphasizes that successional patterns of diversity must be examined in the context of the moisture and elevation gradients.

CHAPTER III

STUDY AREAS

The southern Rocky Mountains extend northward from the Sangre de Cristo range of northern New Mexico and the San Francisco Peaks of Arizona into southern Montana (Peet 1988). The portion in Colorado extends from 37° to 41° N latitude and from 104° 30′ to 109° W longitude. Several large mountain ranges make up this segment of the Rockies, generally trending north-south in the eastern half and being a complex of mountains, plateaus and mesas in the western half (Johnson and Cline 1965). The subalpine forest zone of these mountains and plateaus occupies from ca. 2700 m to an upper timberline at approximately 3450 m (Ramaley 1907, Marr 1961, Peet 1981). The dominant trees are subalpine fir and Engelmann spruce, but in some locations extensive stands of lodgepole pine or quaking aspen may occur.

Four areas of documented past spruce beetle outbreaks (Schmid and Hinds 1974) and/or massive blowdown (Glidden 1981) were selected as part of a larger study quantifying disturbance regimes in

Colorado's Rocky Mountains (Veblen et al. 1989a, 1989b). Eight stands were selected for sampling within Grand Mesa National Forest, Rocky Mountain National Park, Routt National Forest, and White River National Forest (Figure 3.1). Several of these areas suffered other insect outbreaks during the 19th century (Veblen et al. 1989b), but only the most recent disturbances are relevant to this study. Additionally, two control stands were selected in Roosevelt National Forest which has no recent, documented history of spruce beetle outbreak (Figure 3.1). The stands are as follows:

1. Rocky Mountain National Park, Front Range: Hidden Valley-Control (HC) and Hidden Valley-Blowdown (HB).
2. Flattops Wilderness, White River Plateau, White River National Forest: Trappers Lake (TL), Lily Pond Trail (LP) and Ripple Creek Pass (RC).
3. Rabbit Ears Pass, Park Range, Routt National Forest: Walton Creek (WC).
4. Grand Mesa, Grand Mesa National Forest: Cottonwood Lake Trail (CW) and Big Creek Reservoir (BC).
5. Cameron Pass, Front Range, Roosevelt National Forest: Cameron Pass (CP) and Blue Lake Trail (BL).

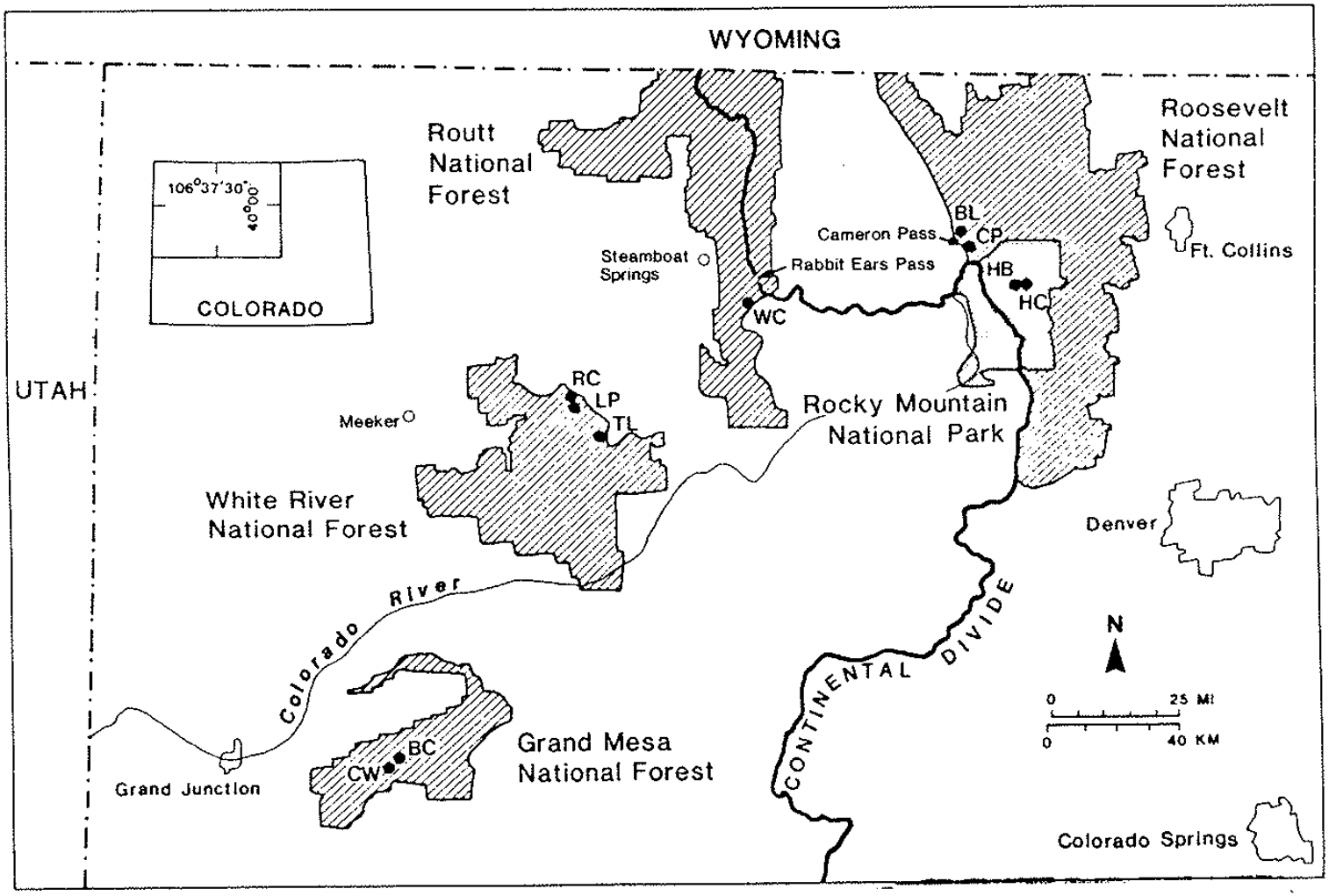

Figure 3.1. Map of the general locations of sampled stands in northwestern Colorado. Abbreviations are: HB (Hidden Valley, blowdown), HC (Hidden Valley, control), CP (Cameron Pass), BL (Blue Lake Trail), TL (Trappers Lake), LP (Lily Pond Trail), RC (Ripple Creek Pass), WC (Walton Creek), CW (Cottonwood Trail), and BC (Big Creek Reservoir).

Geology and Soils

Rising at the western margin of the Great Plains, the Front Range is a belt of mountains about 65 km wide that stretches over 300 km from the Arkansas River in southeast Colorado into Wyoming (Thornbury 1965). The crest of the Front Range forms the Continental Divide in northern Colorado. These mountains are composed primarily of Precambrian granites, gneisses and schists (Lovering and Goddard 1950) that are locally covered with glacial till. Glacial activity has been important in this subalpine region and glacial U-shaped valleys are common. Soils in the Front Range are usually immature, coarse-textured and rocky, and slightly acid (Peet 1981). Lithic orthents are found where bedrock approaches the surface (Johnson and Cline 1965, Peet 1981) and rockiness contributes to soil heterogeneity. Soils in study sites HB, HC, CP and BL are cryoboralfs.

The Park and Gore Ranges, in Routt National Forest, are structurally similar to the Front Range, being faulted anticlines with cores of Precambrian igneous rocks (Chronic and Chronic 1972, Hess and Wasser 1987). Parent material of the study site located in the Park Range (WC) is composed of gneiss and schist.

The White River Plateau lies between the Yampa and Colorado Rivers of northwest Colorado. This is a subalpine, early erosional surface formed by Miocene uplift and subsequent peneplanation (Hess and Wasser 1987). In the northern third of the White River Plateau, where three study sites are located (TL, LP and RC), are basaltic remnants of Miocene and Pleistocene volcanic activity known as the Flattops. Elevations on the Flattops average ca. 3050 m and reach a maximum of 3750 m.

Soils in the subalpine zone of the Park Range and the White River Plateau are commonly cryoboralfs, cryochrepts or cryorthents (Hess and Wasser 1987). Detailed soil surveys have not been conducted for these areas.

Grand Mesa is a high-elevation (up to 3350 m), basaltic plateau in the west-central region of the state. Escarpments and benches are common features, with stream drainage forming numerous small lakes. Detailed soil surveys are not available for this region.

Climate

The climate of the southern Rockies is strongly continental in nature, with sudden extreme changes in weather occurring frequently (Ives 1938, Marr 1961). However, little climatic information is available for

the subalpine zone of Colorado and the locations of the study areas on opposite sides of the Continental Divide make generalizations difficult. Mean annual precipitation in the Colorado subalpine varies from 600 mm to 1000 mm (National Oceanic and Atmospheric Administration 1971) and the number of frost-free days is typically less than 60 (Barry 1972). Baker (1944) compiled a general description of mountain climates for most of the western United States.

Winter weather is the most predictable, with mid-latitude cyclonic storm systems moving into the state from the west carrying Pacific maritime air. Orographic uplift of these air masses results in heavy snowfall in the western mountains of Colorado which thus have a winter maximum of precipitation. Grand Mesa can receive heavy snowfalls, often with accumulations of several meters.

In the spring, moist warm air from the Gulf of Mexico is often uplifted against the east side of the Front Range. High snowfall conditions can occur if cold fronts from the north are present. If polar air is not present, the uplift of moist Gulf air results in continuous, low intensity rainfall. As a result, the east slope of the Front Range experiences a spring maximum of precipitation. Summer precipitation is dominated by local convective thunderstorms which is the

result of moist air from the Gulf of Mexico and tropical Pacific air.

Sample Sites

The locations and descriptions of the ten sampled stands are summarized in Table 3.1. Soil moisture conditions were subjectively assessed by considering elevation, topographic position and aspect, and understory composition. Several understory plant genera are indicators of moist conditions, such as Calamagrostis, Juncus, Mertensia, Mitella, Ranunculus, and Trollius. Other genera are indicative of dry conditions (e.g. Achillea, Astragalus, Drymocallis, Juniperus, Mahonia, Pinus, and Rosa). No stands were poorly drained. Most of the stands are within national parks or wilderness areas and none show any evidence of logging.

Canopy characteristics of the ten stands are summarized in Table 3.2; a more detailed discussion follows for each stand. Age data indicate that none of the stands are less than 200 years of age (Veblen et al. 1989a, 1989b). Understory characteristics and tree regeneration are discussed in Chapter 5 (Results).

Table 3.1. Locations, dates and types of documented disturbance, and characteristics of the ten sampled stands.

Stand	Location[1]	Documented Dates & Types of Disturbance	Elevation	Aspect	Slope	Soil Moisture
HB	RMNP, Sec. 14 T5N, R74W	1973, massive blowdown	2900 m	SW-SSW	15-25	xeric
HC	RMNP, Sec. 14 T5N, R74W	control stand	2900 m	SW-SSW	15-25	xeric
CP	RsNF, Sec. 25 T7N, R76W	control stand	3036 m	S	0-14	well-drained
BL	RsNF, Sec. 2 T7N, R76W	control stand	3018 m	flat with minor S aspect		mesic
TL	WRNF, Sec. 1 T1S, R88W	1940s, spruce beetle outbreak	3000 m	N	11-27	slightly mesic
LP	WRNF, Sec. 4 T1N, R88W	1940s, spruce beetle outbreak	2970 m	rolling	0-14	slightly mesic
RC	WRNF, Sec. 28 T2N, R88W	1940s, spruce beetle outbreak	3150 m	NW	0-5	well-drained
WC	RtNF, Sec. 26 T5N, R83W	1940s, spruce beetle outbreak	3048 m	NE	2-10	locally mesic
CW	GMNF, Sec. 26 T11S, R95W	1940s, spruce beetle outbreak	3304 m	NW	0-17	slightly mesic
BC	GMNF, Sec. T11S, R94W	1940s, spruce beetle outbreak	3085 m	N-NE	2-17	mesic

[1]RMNP = Rocky Mountain National Park
WRNF = White River National Forest
RtNF = Routt National Forest
GMNF = Grand Mesa National Forest
RsNF = Roosevelt National Forest

Table 3.2. Canopy characteristics of the ten sampled stands. Values are the percent of total live basal area and density and the percent of total dead basal area and density represented by each tree species. (A = *Abies lasiocarpa*, E = *Picea engelmannii*, C = *Pinus contorta*, Lv = live trees, Dd = dead-standing trees).

Stand		Percent of Basal Area			Percent of Density		
		A	E	C	A	E	C
HB	Lv-	53	19	27	79	12	9
	Dd-	12	25	63	22	4	74
HC	Lv-	8	6	86	27	6	67
	Dd-	1	1	98	3	2	95
CP	Lv-	24	44	32	53	36	11
	Dd-	69	4	27	79	8	13
BL	Lv-	27	73		47	53	
	Dd-	48	52		60	40	
TL	Lv-	68	12	20	70	26	4
	Dd-	8	34	58	20	31	49
LP	Lv-	64	36		70	30	
	Dd-	20	80		52	48	
RC	Lv-	83	17		76	24	
	Dd-	39	61		56	44	
WC	Lv-	78	22		73	27	
	Dd-	29	71		71	29	
CW	Lv-	39	61		59	41	
	Dd-	94	6		84	16	
BC	Lv-	53	47		62	38	
	Dd-	84	16		86	14	

Blowdown and Control (Stands HB and HC)

The two stands in Rocky Mountain National Park are located in Hidden Valley on the east slope of the Front Range (Veblen et al. 1989b). Stand HB suffered severe blowdown in 1973 while adjacent stand HC was only slightly affected and serves as a control for comparison. The soils are rocky cryoboralfs derived from granitic parent materials and have O horizons 0 to 10 cm thick. Charcoal is abundant in the upper soil layers in both stands.

Stand HB had thousands of trees blowndown by hurricane force winds in May 1973 (Glidden 1981, Veblen et al. 1989a). Presently, it is characterized by sparse, remnant lodgepole pine and spruce up to 47 cm dbh, but mostly < 30 cm dbh. Fir is abundant and generally < 20 cm dbh. Basal area and density of live trees are the lowest of any of the sampled stands (Tables 3.3 and 3.4). Dead-standing trees are primarily lodgepole pine, and to a lesser extent, spruce (Table 3.2). Orientation of the logs in HB reveals that the winds came from the west to southwest. During the first half of 1974, maximum windspeed was recorded at 142 km per hour and 9% of the days had gusts > 103 km per hour (Glidden 1981).

Stand HC was largely unaffected by the 1973 blowdown and has a much higher basal area of live trees

Table 3.3. Basal area (m^2/ha) of live and dead-standing trees for all stands, by species. Dead includes dead-standing trees and stumps.

Stand	Species	Basal Area Live	Dead	Total
HB	A. lasiocarpa	8.7	1.4	10.1
	P. engelmannii	3.1	3.0	6.1
	P. contorta	4.4	7.4	11.8
	Total	16.2	11.8	28.0
HC	A. lasiocarpa	4.0	0.1	4.1
	P. engelmannii	2.7	0.1	2.8
	P. contorta	41.4	10.9	52.3
	Total	48.1	11.1	59.2
CP	A. lasiocarpa	13.1	5.4	18.5
	P. engelmannii	24.7	0.3	25.0
	P. contorta	18.1	2.1	20.2
	Total	55.9	7.8	63.7
BL	A. lasiocarpa	11.2	8.2	19.4
	P. engelmannii	30.9	8.8	39.7
	Total	42.1	17.0	59.1
TL	A. lasiocarpa	13.5	2.0	15.5
	P. engelmannii	2.5	8.2	10.7
	P. contorta	3.9	14.1	18.0
	Total	19.9	24.3	44.2
LP	A. lasiocarpa	20.5	3.9	24.4
	P. engelmannii	11.6	15.3	26.9
	Total	32.1	19.2	51.3

Table 3.3 (continued)

Stand	Species	Basal Area Live	Dead	Total
RC	A. lasiocarpa	30.3	5.7	36.0
	P. engelmannii	6.4	8.9	15.3
	Total	36.7	14.6	51.3
WC	A. lasiocarpa	35.8	3.8	39.6
	P. engelmannii	10.3	9.2	19.5
	Total	46.1	13.0	59.1
CW	A. lasiocarpa	22.3	8.5	30.8
	P. engelmannii	35.0	0.5	35.5
	Total	57.3	9.0	66.3
BC	A. lasiocarpa	24.9	11.3	36.2
	P. engelmannii	21.8	2.1	23.9
	Total	46.7	13.4	60.1

Table 3.4. Densities (number/ha) of live and dead-standing trees for all stands, by species. Dead includes dead-standing trees and stumps.

Stand	Species	Density		
		Live	Dead	Total
HB	A. lasiocarpa	658	52	710
	P. engelmannii	100	10	110
	P. contorta	77	171	248
	Total	835	213	1068
HC	A. lasiocarpa	248	7	255
	P. engelmannii	52	4	56
	P. contorta	604	193	797
	Total	904	204	1108
CP	A. lasiocarpa	888	187	1075
	P. engelmannii	600	19	619
	P. contorta	175	31	206
	Total	1663	227	1395
BL	A. lasiocarpa	943	129	1072
	P. engelmannii	1079	85	1164
	Total	2022	214	2236
TL	A. lasiocarpa	1105	87	1192
	P. engelmannii	418	132	550
	P. contorta	59	208	267
	Total	1582	427	2009
LP	A. lasiocarpa	1155	85	1240
	P. engelmannii	485	80	565
	Total	1640	165	1805

Table 3.4 (continued)

Stand	Species	Density Live	Dead	Total
RC	A. lasiocarpa	1650	100	1750
	P. engelmannii	515	80	595
	Total	2165	180	2345
WC	A. lasiocarpa	952	171	1123
	P. engelmannii	348	71	419
	Total	1300	242	1542
CW	A. lasiocarpa	1015	305	1320
	P. engelmannii	695	60	755
	Total	1710	365	2075
BC	A. lasiocarpa	727	195	922
	P. engelmannii	441	32	473
	Total	1168	227	1395

than in HB (Table 3.3). Lodgepole pine dominates in both basal area and density, ranging up to 58 cm dbh, while fir is common in the subcanopy (Table 3.2). Spruce is scarce and, along with fir mostly < 30 cm dbh.

Control Stands (Spruce Beetle)

Stands CP and BL

No recent past outbreaks of bark beetle have been documented for the area of the Front Range in which these two stands are located. They were chosen ascontrols for comparison with the other stands.

Stand CP occupies a mid-slope position on a rolling hillside, with several intermittent streambeds running through the stand. Soil is well-drained, thin and rocky, derived from glacial till. Logs are infrequent and pit and mound topography is not well-developed. Several large, burned out stumps were foundin the stand.

In stand CP lodgepole pine occurs in the canopy, and is represented by a few large, old trees (Veblen et al. 1989b). Live and total basal areas are high (Table 3.3) of which spruce is nearly 50% (Table 3.2). Fir accounts for slightly > 50% of the density of live trees, but has a low basal area, reflecting a large number of small diameter trees. Seventy-nine percent of the dead-standing trees are fir. Maximum ages of all

three species are < 250 years.

Stand BL is located on a slightly sloping terrace of till and is moderately well-drained. The terrace surface slopes towards a creek and in some locations a small moisture gradient can be seen, with mesic conditions in the stand and drier conditions towards the edge of the terrace. Logs, including some decomposed ones, are common. Pit and mound microtopography is well-developed.

There is no lodgepole pine in stand BL. The total density is high, with spruce representing 53% of the density of live trees (Table 3.4). Basal area is also high (Table 3.3) with spruce dominating (Table 3.2). Fir is also abundant, yet its basal area is much lower. Maximum ages are > 310 years (Veblen et al. 1989b). Dead-standing basal area is equally divided between spruce and fir, but fir has a greater number of dead stems.

Spruce Beetle-Disturbed Stands

Stands TL, LP and RC

During the 1940s the White River Plateau suffered a major outbreak of spruce bark beetle that killed nearly all spruce > 20 cm dbh (Schmid and Hinds 1974). Charcoal is present or abundant in all three of the stands.

In stand TL soils are rocky and have thin O horizons. Soil moisture is slightly mesic, with local small springs, made apparent by an increase in understory cover and a change in species composition in moist areas. The presence of lodgepole pine implies that this is a relatively xeric site even though there are mesic patches due to the small springs. Fallen trees are common, though large, decomposing logs are rare.

In stand TL subalpine fir comprises more than half of the live basal area and density, while lodgepole pine and Engelmann spruce dominate the dead-standing basal area (Table 3.2). Lodgepole pine is represented by a few large, remnant trees up to 43 cm dbh and many dead-standing stems (Tables 3.3 & 3.4). Subalpine fir is abundant as smaller, subcanopy trees mostly < 20 cm dbh. Spruce is less common and generally < 15 cm dbh.

Stand LP has rolling topography, with all slope positions represented. A small, shallow ravine crosses the transect at 60 m. Soil moisture is slightly mesic, however there is no indication of small springs as in stand TL. Fallen trees are common and generally large (> 30 cm dbh), while pit and mound microtopography is slight.

The canopy of stand LP is patchy and lacks lodgepole, with fir dominating the basal area and

density of live trees (Table 3.2). The density of live trees is high, as is the live basal area. Dead-standing spruce are few and large, as indicated by their high basal area but low density (Tables 3.3 & 3.4).

Stand RC occupies a well-drained, midslope position. Old, large decomposing logs and more recently fallen trees are common, contributing to a thick O horizon. Pit and mound microtopography is strongly developed. Grazing of sheep may be a factor for this stand, since nearby areas are used for summer pasturing. However, no evidence of recent grazing was seen in the stand.

Stand RC is a dense stand composed of abundant fir and less abundant spruce, both generally < 15 cm dbh (Tables 3.3 & 3.4). Fir dominates in both basal area and density of live trees (Table 3.2). Dead-standing basal area is relatively high for both species, but the dead spruce are larger than the fir. Age data indicate that this stand is probably < 250 years old (Veblen et al. 1989b).

Stand WC

Schmid and Frye (1977) documented an outbreak of spruce beetle in the vicinity of Rabbit Ears Pass, Routt National Forest, during the 1940's. Up to 40% of the Engelmann spruce were killed by this outbreak.

Stand WC occupies a moderately steep mid-slope. Small depressions in the slope form locally mesic microsites, and high soil organic matter facilitates the retention of moisture. Pit and mound microtopography is strongly developed. Large, decomposing logs contribute much organic matter to the soil.

WC is another stand dominated by fir (Table 3.2). Overall, density is moderate but basal area is high for live trees (Tables 3.3 & 3.4). The trees in this stand are larger and older than in the White River National Forest stands, with maximum ages over 300 years for fir (Veblen et al. 1989b). Dead-standing spruce are few, but large and may have been as old as the live fir at the time of death. There are a moderate number of small, dead-standing fir.

Stands CW and BC

Grand Mesa suffered outbreak conditions of spruce beetle in the 1940's, during which up to 50% of the large spruce were killed in some locations (Schmid and Hinds 1974). Exposed basaltic boulders and cobbles are common, as are depressions within the parent material.

Stand CW occupies a rolling, midslope position. The stand is moderately well-drained, but not xeric. Logs are rare and some are large and decomposed. Little

evidence of fire was found.

Stand CW supports a very high basal area of live trees (Table 3.3), of which spruce accounts for more than 50% (Table 3.2). Tree density is also very high, with fir predominant (Table 3.4). Dead-standing spruce are scarce, while dead fir are more common. The main canopy trees are larger, older spruce, which dominates in basal area. The subcanopy is primarily fir, which dominates in density.

In stand BC topography is rolling along the slope, with small depressions. The drainage is poor and small, ephemeral ponds occur in the vicinity of the transect. Boulders and rocks are exposed in many locations. Large, decomposed logs are common and pit and mound microtopography is strongly developed. Small amounts of charcoal were found in treefall pits.

Despite the mesic site, both density and basal area of live trees are lower in BC than in CW (Tables 3.3 & 3.4). Total density is also much lower, however total basal area is similar to that for CW. Fir dominates in both live basal area and density (Table 3.2) and additionally accounts for most of the dead-standing trees. Age and size data reveal that the spruce are larger than the fir and reach older maximum ages of > 300 years (Veblen et al. 1989b).

CHAPTER IV

METHODS

Study areas had to be chosen to sample disturbed forests and in this regard were subjectively chosen. Based on field reconnaissance, ten stands were selected for sampling within these general areas: Grand Mesa National Forest (CW and BC), Rocky Mountain National Park (HB and HC), Routt National Forest (WC), Roosevelt National Forest (CP and BL), and White River National Forest (TL, LP, and RC).

To understand the response of understory plant communities to disturbance severity, comparisons were made with control old-growth stands where there was no evidence of similar past disturbance. For the purposes of this study, old-growth refers to stands with trees $\geq$ 200 years old and lacking recent major canopy disturbance.

Because of the large regional extent of the 1940s spruce beetle outbreak, unlogged control stands were difficult to locate near the disturbed stands. The controls for the beetle-disturbed stands are located at some distance, in Roosevelt National Forest. Only in

the case of the Hidden Valley blowdown stand is the control stand located adjacently. This somewhat limits comparisons that can be made among stands.

Field Methods

Transects and Plots

Once study stands were chosen, one transect of 300 m was used in each stand, with 10 plots systematically placed every 30 m along the transect. The starting point of each transect was randomly chosen. The direction of each transect was chosen to sample a homogeneous stand, subjectively determined by walking through the area. Plot sizes varied from 5x10 m to 20x40 m, so that each plot contained an average of about 20 live trees $\geq$ 4 cm dbh. As a result of the varying plot size, the area sampled in each stand varied from .14 ha to .31 ha. Elevation, slope, aspect and topographic position were recorded for each stand. Also noted were general stand characteristics, such as rockiness and the presence of charcoal.

In each plot along a transect, species and dbh were recorded, for all live and dead-standing trees. Dead-standing trees included wind-snapped trees taller than 1.4 m in height. Species and dbh of stumps were also recorded. Logs $\geq$ 15 cm dbh, which crossed the transect line, were recorded and species determined if

possible. Saplings, defined as > 1.4 m tall but < 4 cm dbh, were counted for each species.

Understory Quadrats

Ten 1x1 m quadrats were located in a restricted-random fashion in each plot. Half of the quadrats were randomly located on each side of the transect line, which bisected all plots. Within each quadrat, percent cover was estimated for each understory vascular plant species encountered, using a modified Braun-Blanquet cover class method (Mueller-Dombois and Ellenberg 1974). A value of 5 was equivalent to 76-100%, 4 = 51-75%, 3 = 26-50%, 2 = 6-25%, 1 = 1-5% and + = < 1%. Other species occurring within the stand but not encountered in the quadrats were recorded as present. Cover values were also assessed for bare mineral soil, litter, rocks, and non-vascular plants (mosses, lichens and liverworts). Additionally, counts were made of tree seedlings in two height classes (< 20 cm and 20-140 cm) and of the number of seedlings established on logs.

Sampling was completed between June 15 and August 15, 1987. A species list was compiled for each stand and voucher specimens were deposited with the University of Colorado Museum herbarium. Nomenclature follows Weber (1976, 1988). A few species pairs were difficult to distinguish and were therefore lumped as a

single species. Arnica cordifolia and Arnica latifolia were lumped as A. cordifolia. All Rosa, Fragaria, Cirsium and Juncus species were lumped into their respective genera. A few composite and graminoid species remain unidentified due to the lack of flowering parts or sufficient vegetative material for identification purposes.

Diffuse Site Factor

To quantify tree canopy cover, hemispherical canopy photographs were taken from a height of 1.9 m every 30 m along each transect, starting at the 10 m point. Slide film was used with a 180°, 8 mm lens on a 35 mm camera body. The slides were projected upon a template divided into one-thousand segments. Each segment was classified according to the amount it was blocked by the canopy, in the following percentage classes: 100% blocked; 99-67%; 66-34%; 33-<1%; and 0% blocked. Percent diffuse light was derived for each template by determining the number of divisions blocked by each percentage class. The percent diffuse light for the 11 templates was averaged to obtain a diffuse site factor for each stand (Anderson 1964). The diffuse site factor is proportional to the total incident radiation, which is inversely proportional to canopy cover. Thus, a high diffuse site factor indicates an open canopy and greater disturbance severity.

Analytical Methods

Disturbance Parameters

Three methods were used to quantify severities of canopy disturbance: tree mortality (% dead-standing); diffuse site factor; and fallen trees.

Dead-standing Basal Area and Density. Percent dead-standing basal area was calculated for each tree species and as an average for the stand. Percent dead-standing density was also calculated using the following equation:

$$\%\ \text{Dead-standing Basal Area} = \frac{\text{Basal area of dead-standing trees}}{\text{Total basal area}}. \quad (1)$$

Where total basal area is the basal area of all live and dead-standing trees. Percent dead-standing density was calculated the same way, replacing basal area with density in the above equation. This value is indicative of recent tree mortality (i.e. within the past $\pm$ 60 years) as reflected by the proportion of dead-standing trees.

Diffuse site factor. The second disturbance parameter used is the diffuse site factor, calculated for each stand as a mean and standard deviation. These were tested for independence using Duncan's multiple range ANOVA (SAS Institute Inc. 1985).

Fallen Trees. The third indicator of disturbance severity is based on the number of logs intercepted by the transect line. The number and basal area, by species and total, were calculated for each stand. Since the sample was not 100% of the logs, basal area for logs is in units of m^2/100 m, the distance of the transect in plots.

Understory Cover and Richness

Understory data were summarized by a simple life-form classification (Whittaker 1975). The categories used are shrubs, forbs, graminoids, and non-vascular plants (bryophytes and thallophytes). Mean percent cover was calculated for each understory species for each plot, then summed to obtain mean percent cover values for each plot in each life-form category. Non-vascular plants were not identified, but were lumped in their respective groups. Plot values were averaged to obtain mean percent cover ($\pm$ standard deviation) by life-form for each stand. Total understory cover was calculated by summing values for shrubs, forbs and graminoids.

Understory richness is the total number of vascular plant species occurring in the sampled quadrats (no./100 m^2 or .01 ha), summed both for plots and the stand. For the purposes of the Spearman rank

correlations, richness was determined separately for shrub richness and herb richness.

Tree Seedlings and Saplings

Densities (no./ ha) of seedlings and saplings, by species, were subjected to a Mann-Whitney U test to determine if the mean number of seedlings or saplings was significantly different (Siegel 1956). This was done both between species within a stand and for the same species between stands. Lodgepole seedlings and saplings were to infrequent to perform statistical tests.

The frequency of seedlings established on logs was compared using two-by-two contingency tables. Yates' corrected chi-square test was used, or the Fischer exact test was used when sample sizes were small (Siegel 1956, NH Analytical Software 1985).

Spearman Rank Correlations

The non-parametric Spearman rank correlation coefficient (r) was chosen for correlation analysis (NH Analytical Software 1985). To test the relationships between the canopy and the understory (including tree seedlings and saplings), Spearman rank correlation coefficients were calculated for a set of canopy and understory variables within each stand. N = 10 in all cases, as there are 10 plots in each stand. All

possible pairs were tested.

Canopy variables (and abbreviations used for them in the tables), included: basal area, by species (A = A. lasiocarpa, E = P. engelmannii, C = P. contorta), of live and dead-standing trees (Lv = Live basal area, Dd = dead-standing basal area) and total live (LvTTL) and dead (DdTTL) basal areas. Basal area of logs was added to dead-standing basal area (Dwl = dead with logs added) as an additional variable.

Understory variables included: percent cover, by life-form (SHRBCVR = shrub cover, FRBCVR = forbs, GRMCVR = graminoids and NONVCVR = non-vascular plants), and total cover (TTLCVR); shrub, herb and total richness (SHRBSPP, HRBSPP, RCHNES); seedling density, by species; and sapling density, by species (SEEDS = seedlings and SAPS = saplings). Litter cover (LTRCVR) and percent rockiness (RKINES) are also used.

To test whether intra-stand patterns of association are consistent with inter-stand patterns, the mean values of each variable for each stand were combined into one data set and Spearman rank correlations again calculated. Three variables were added to this data set: the diffuse site factor (DIFFSE) for each stand; and the percent of fir and spruce seedlings on logs (ASDSOL and ESDSOL).

Similarity Indices

The similarity of each pair of plant communities represented by the sampled stands was tested using similarity indices (Mueller-Dombois and Ellenberg 1974). Sorenson's Index of Similarity was applied to each pair of stands, using:

$$IS = \frac{2c}{A + B} \times 100. \qquad (2)$$

Here, c is the number of species found in both stands, A is the number of species found in stand A and, B is the number of species found in stand B.

The similarity of two plant communities is also a function of the abundance of each species present, in this case percent cover. For this reason, Sorenson's Community Coefficient was also calculated for each pair of stands (Mueller-Dombois and Ellenberg 1974), where:

$$CC = \frac{2Mw}{MA + MB} \times 100 \ . \qquad (3)$$

Here, Mw is the sum of the smaller cover values of the species in common to the two stands, MA is the sum of the cover values for all species in stand A, and MB is the sum of the cover values for all species in stand B.

CHAPTER V

RESULTS AND INTERPRETATION

Disturbance Parameters

The results for percent dead-standing basal area, the diffuse site factor and intercepted logs indicate that the severity of disturbance in these stands varies greatly. Several stands were severely disturbed by windthrow and/or beetle outbreaks, while others show little if any disturbance by these agents.

Blowdown Stand (HB) & Control Stand (HC)

Stand HB was one of the most severely disturbed of the ten, though the disturbance was of a different type than that occurring in the others. All three of the disturbance parameters indicate an intense, but localized disturbance.

In stand HB, the percent dead-standing basal area is highest for lodgepole and spruce, with fir showing low mortality (Table 5.1). Together, spruce and lodgepole together account for 88% of the dead-standing basal area and 85% of the dead-standing density. The high mortality of spruce and lodgepole is primarily a result of wind-snap among main canopy trees.

Table 5.1. Percent dead-standing basal area and density, by species, for all ten sampled stands.

Stand	Species	% Dead-standing Basal Area	% Dead-standing Density
HB	A. lasiocarpa	14	7
	P. engelmannii	49	9
	P. contorta	63	69
	Total	42	20
HC	A. lasiocarpa	2	3
	P. engelmannii	2	7
	P. contorta	21	24
	Total	19	18
CP	A. lasiocarpa	29	17
	P. engelmannii	1	3
	P. contorta	10	15
	Total	12	13
BL	A. lasiocarpa	42	12
	P. engelmannii	22	7
	Total	29	10
TL	A. lasiocarpa	13	7
	P. engelmannii	77	24
	P. contorta	78	78
	Total	55	21
LP	A. lasiocarpa	16	7
	P. engelmannii	57	14
	Total	37	9

Table 5.1 (cont)

Stand	Species	% Dead-standing Basal Area	% Dead-standing Density
RC	A. lasiocarpa	16	6
	P. engelmannii	58	13
	Total	29	8
WC	A. lasiocarpa	10	15
	P. engelmannii	47	17
	Total	22	16
CW	A. lasiocarpa	28	23
	P. engelmannii	1	8
	Total	14	18
BC	A. lasiocarpa	31	21
	P. engelmannii	9	7
	Total	22	16

In contrast, the total percent dead-standing basal area is low for HC, with lodgepole pine accounting for 98% of this (Table 5.1). Such high basal areas of dead-standing lodgepole pine (Table 3.3) are typical of self-thinning stands (Peet 1981, Veblen 1986).

The nearly tenfold greater density and basal area of live lodgepole pine in HC compared to HB (Tables 3.3 & 3.4) is an indication of the severity of disturbance in stand HB. The much greater frequency and basal area of intercepted logs in HB versus HC also reflects the severity of the blowdown (Table 5.2).

Comparing canopy covers by use of the diffuse site factor allows an additional assessment of the disturbance severity. Stand HB has a 1.75 times more open canopy than stand HC (Table 5.3). The hemispherical view of the lens includes many relatively short trees. Therefore, the difference seen here is a conservative measure of the severity of canopy disturbance in stand HB.

Control Stands (Spruce Beetle)

Stands Cameron Pass (CP) & Blue Lake Trail (BL).

In both stands CP and BL the mortality of fir is higher than for either spruce or lodgepole (Table 5.1). However, the total percent basal area of dead-standing trees in stand CP is only 12%, the lowest of any of the

Table 5.2. Basal area (m^2) and frequency of logs intercepted by the transects in the ten sampled stands, by species. Sampled distance = 100 m.

Basal Area

Stand	Abies lasiocarpa	Picea engelmannii	Pinus contorta	Unidentified	Total
HB	0.25	0.16	1.44		1.85
HC		0.06	0.79		0.85
CP	0.06		0.04		0.10
BL	0.77	1.07			1.84
TL	0.17	1.44	1.38	0.39	3.38
LP	0.24	2.81		0.08	3.13
RC	0.60	1.40		0.31	2.31
WC	0.53	0.41		0.11	1.05
CW	0.37	0.05		0.16	0.58
BC	2.96	0.94		0.32	4.22

Frequency

	Stand									
Species	HB	HC	CP	BL	TL	LP	RC	WC	CW	BC
A. lasiocarpa	2		3	14	6	5	12	5	8	27
P. engelmannii	3	1		8	19	24	20	3	1	8
P. contorta	38	11	2		25					
Unidentified					7	2	6	2	3	3
Total	43	12	5	22	57	31	38	10	12	38

Table 5.3. Diffuse site factor (mean + standard deviation) for all sampled stands. n = the number of hemispherical photos used in the calculations. Means followed by the same letter are not statistically different (Duncan's multiple range ANOVA, $P \leq .01$).

Stand	n	Diffuse Site Factor (+ SD)	
HB	11	73.8 (± 12.7)	
HC	11	43.0 (± 5.2)	bc
CP	11	39.1 (± 6.2)	ab
BL	11	37.3 (± 6.8)	a
TL	11	59.5 (± 8.3)	
LP	10	45.8 (± 8.1)	bc
RC	11	49.8 (± 12.4)	c
WC	11	41.5 (± 5.5)	ab
CW	11	40.3 (± 5.7)	ab
BC	11	39.0 (± 5.0)	ab

stands. Both spruce and fir are relatively young in this seral stand and consequently mortality is lower. Stand CP shows no indication of disturbance by spruce beetle.

The percent dead-standing basal area for spruce in stand BL is much higher than that found in stand CP (Table 5.1). Stand BL is much older than stand CP, with some spruce greater than 400 years of age. All of the dead spruce had bark beetle galleries indicating an endemic population of beetles, but there is no evidence of an epidemic outbreak.

Both CP and BL have low diffuse site factors (Table 5.3). Of the two stands, BL has a higher frequency of logs, as expected for an old-growth stand (Table 5.2).

Spruce Beetle-Disturbed Stands

White River: Stands Trappers Lake (TL), Lily Pond (LP), & Ripple Creek Pass (RC). All three of the stands chosen for sampling in the Flattops Wilderness suffered high spruce mortality during the 1940s outbreak. Percent dead-standing basal area for spruce varies from 57% (LP) to 77% (TL) (Table 5.1).

Stand TL includes a large component of dead lodgepole pine (Tables 3.3 & 3.4), many of which were killed in the 1940s outbreak (Schmid and Hinds 1974) and some of which may have been killed by a current outbreak of mountain pine beetle. Engelmann spruce and lodgepole pine together make up 92% of the total dead-standing basal area (Tables 3.3 & 3.4). Mortality of spruce is primarily the result of spruce beetle attack. Some of the lodgepole mortality may be due to self-thinning and successional development of the stand. While total basal area of live trees is similar to that in HB (Table 3.3), the dead-standing basal area is much greater in TL.

The diffuse site factor of 59.5% for TL indicates a severely disturbed stand. Additionally, there is a high frequency of intercepted logs at stand TL (Table 5.2). By far the most are spruce and lodgepole.

Percent dead-standing basal area for spruce in stands LP and RC is lower than in stand TL (Table 5.1). In both LP and RC, this value for spruce is greater than 50%, while for fir it is less than 20%.

Both stands LP and RC have relatively high numbers and basal areas of intercepted logs (Table 5.2), of which most are spruce. The diffuse site factors are high for the two stands (Table 5.3).

Based on the above measures of disturbance, all three of the stands in the Flattops Wilderness were severely disturbed by the most recent beetle outbreak.

Rabbit Ears Pass: Stand Walton Creek (WC). This stand was slightly affected, if at all by the 1940s outbreak of spruce bark beetle. The intermediate percent dead-standing basal area of Engelmann spruce is the result of a few, large trees (Table 5.1). Few logs were intercepted by the transect (Table 5.2). Schmid and Hinds (1974), however, describe the general area as being moderately affected by the 1940s outbreak. The diffuse site factor for WC is relatively low (Table 5.3), a result of the relatively high basal area of live trees (Table 3.3).

Grand Mesa: Stands Cottonwood Trail (CW) & Big Creek Reservoir (BC). In stand CW, the low percent dead-standing basal area for spruce indicates a stand

unaffected by bark beetle (Table 5.1). In stand BC spruce mortality is greater than in CW, and the basal area and number of fallen spruce are substantially greater (Table 5.2). In contrast to stand CW, stand BC was significantly affected by the 1940s outbreak. This conclusion is supported by tree growth patterns in the two stands (Veblen et al. 1989b).

Both of these stands have low diffuse site factors (Table 5.3). In CW, this reflects the high density, combined with low spruce mortality and the fact that the dead fir are predominantly subcanopy. In BC, it is a result of the high basal area.

Understory Structure and Composition

There is much variability in the understory both within and between stands. Most understory species are rare and occur in only one stand. Only a few are common, occurring in eight or more stands. A total of 114 understory species (not counting trees) occupy the ten sampled stands. Of these, 15 are shrubs, 77 are forbs, and 22 are graminoids. Additionally, there are many species of mosses and lichens, but no attempt was made to identify these.

Hidden Valley Stands

Stands HB and HC have the lowest understory cover of the ten stands, which can be attributed to the xeric nature of the stands (Table 5.4). Richness is also low (Table 5.6). HB has higher total cover than HC but this increase in the disturbed stand is distributed differently among the life-forms. In HB, shrub cover is slightly less than in HC, but cover of forbs and graminoids together is 73% higher in HB than HC.

In HB, 49% of the understory cover is contributed by shrubs, of which 5 species have nearly equal abundance (Table 5.5). In contrast, in HC shrubs represent 80% of the understory cover, of which J. communis and V. myrtillus are the most abundant (Table 5.5). In both stands, Arnica cordifolia was the most abundant forb species.

The difference between the understories of these two stands is most apparent in the structure, with dominance shifting from shrubs in HC to forbs and graminoids in HB. However, much of the increase in forb cover in HB is the result of a single plot which includes a small seep, where forb and moss cover are both high. If the effect of this plot is removed from the data, then mean forb cover for HB is 2.20%, mean graminoid cover is 3.20%, and mean shrub cover is 8.3%. This indicates that graminoids may be the only stratum

Table 5.4. Mean understory cover (± SD), by life-form, for each of the ten stands. Total cover does not include non-vascular plants.

Stand	Life Forms									
	Shrubs		Forbs		Graminoids		Total		Non-vascular	
HB	8.4	(± 5.0)	5.6	(± 11.1)	3.2	(± 3.9)	17.2	(± 13.4)	3.2	(± 5.4)
HC	9.3	(± 4.6)	2.1	(± 2.4)	0.3	(± 0.2)	11.7	(± 5.7)	2.4	(± 4.4)
CP	47.5	(± 17.7)	9.7	(± 9.0)	0.5	(± 0.6)	57.7	(± 15.6)	8.9	(± 3.8)
BL	25.5	(± 13.9)	33.6	(± 17.8)	5.5	(± 3.1)	64.6	(± 11.4)	17.1	(± 7.0)
TL	21.6	(± 10.7)	25.4	(± 11.3)	0.2	(± 0.5)	47.3	(± 14.8)	12.2	(± 10.1)
LP	7.5	(± 5.9)	37.3	(± 13.3)	8.8	(± 6.0)	53.7	(± 20.5)	11.1	(± 8.6)
RC	44.4	(± 9.6)	15.9	(± 8.6)	4.5	(± 5.7)	64.8	(± 11.9)	5.3	(± 3.2)
WC	40.1	(± 9.3)	9.8	(± 14.4)	5.7	(± 4.4)	55.5	(± 13.0)	17.2	(± 10.4)
CW	12.9	(± 6.4)	5.7	(± 4.3)	1.1	(± 1.2)	19.8	(± 7.3)	13.1	(± 7.7)
BC	19.3	(± 6.2)	42.7	(± 14.2)	4.3	(± 2.3)	66.1	(± 17.5)	14.7	(± 8.6)

Table 5.5. Mean cover (%) and percent frequency (number of quadrats out of 100) of vascular plant species for each of the ten stands. Life-forms are classified as: F= forb, G= graminoid, S= shrub. Freq. = frequency.

Species	Life Form	Stand HB		Stand HC	
		Cover	Freq.	Cover	Freq.
Achillea lanulosa	F	0.19	2	0.01	1
Arnica cordifolia	F	2.96	21	1.32	18
Boechera drummondii	F			0.01	1
Chamerion angustifolium	F	0.47	4		
Drymocallis fissa	F	0.85	5	0.16	1
Fragaria spp.	F	0.01	1		
Geranium richardsonnii	F	0.04	3	0.03	1
Oreochrysum parryi	F	0.33	10	0.21	5
Packera fendleri	F	0.69	3	0.07	3
Pyrola chlorantha	F	0.01	2		
Pyrola minor	F			0.17	14
Ramischia secunda	F			0.10	5
Sedum lanceolatum	F			0.03	1
Unknown a.	F	0.01	1		
Carex rossii	G	2.59	26	0.26	16
Juncus spp.	G	0.04	1		
Luzula parviflora	G	0.51	6		
Poa fendleriana	G	0.06	2	0.03	1
Arctostaphylos uva-ursi	S	1.00	5	0.16	1
Jamesia americana	S			0.16	1
Juniperus communis	S	1.55	7	5.36	22
Mahonia repens	S	0.36	7		
Rosa spp.	S	1.49	14	0.88	21
Rubus idaeus	S	1.60	15		
Sambucus racemosa	S	0.35	5		
Vaccinium myrtillus	S	2.09	23	2.69	28

Table 5.5 (continued)

Species	Life Form	Stand CP Cover	Stand CP Freq.	Stand BL Cover	Stand BL Freq.
Achillea lanulosa	F	0.01	1		
Angelica pinnata	F			0.58	21
Antennaria spp.	F	0.04	3		
Aquilegia elegantula	F	0.06	2	0.41	12
Arnica cordifolia	F	3.56	55	10.37	100
Arnica parryi	F	0.13	5	1.16	21
Aster foliaceus	F	0.03	1		
Astragalus alpinus	F			0.03	1
Caltha leptosepala	F			0.22	4
Castilleja spp.	F			0.04	3
Chamerion angustifolium	F	0.02	4	0.38	6
Chlorocrepis albiflora	F	0.01	1		
Chlorocrepis tristis	F	0.48	25	0.22	14
Cirsium spp.	F	0.04	2		
Delphinium barbeyi	F			1.51	21
Erigeron coulteri	F	0.01	1	0.03	1
Erigeron eximius	F	1.00	24	3.71	57
Erythronium grandiflorum	F	0.29	13	0.78	35
Fragaria spp.	F	0.49	7	0.35	15
Gentianella amarella	F	0.06	6	0.06	6
Geranium richardsonnii	F	0.03	1		
Ligusticum porteri	F	1.19	32	2.22	39
Listera cordata	F	0.01	1	0.10	4
Mertensia ciliata	F			0.22	3
Mitella pentandra	F			0.29	7
Moneses uniflora	F			0.33	11
Noccaea montana	F	0.01	1		
Oreochrysum parryi	F	0.31	7	0.81	18
Osmorhiza depauperata	F	0.45	4	1.22	33
Pedicularis bracteosa	F	0.30	10	0.15	10
Pedicularis racemosa	F	0.03	1	0.36	12
Potentilla spp.	F	0.01	1		
Pseudocymopteris montanus	F	0.24	8	1.54	37
Ramischia secunda	F	0.06	2	0.71	17
Ranunculus spp.	F			0.01	1
Senecio crassulus	F	0.04	7	0.16	7
Senecio triangularis	F			0.28	5
Sibbaldia procumbens	F	0.19	3		
Smilacina stellata	F			0.60	9
Solidago spathulata	F	0.01	2		
Taraxacum officinale	F	0.03	1		
Trollius albiflorus	F			3.81	41
Unknown j.	F	0.16	1		
Unknown k.	F			0.31	2
Unknown l.	F			0.12	4
Unknown m.	F			0.03	1
Zigadenus elegans	F	0.41	11	0.45	20
Bromopsis canadensis	G			0.33	15
Calamagrostis canadensis	G			0.22	10
Carex geyeri	G			2.69	42

Table 5.5 (continued)

Species	Life Form	Stand CP Cover	Stand CP Freq.	Stand BL Cover	Stand BL Freq.
Carex nova	G			0.19	2
Carex rossii	G	0.45	15	0.31	12
Elymus glaucus	G			0.50	14
Grass BL10	G			0.19	2
Grass BL11	G			0.16	7
Grass CP2	G	0.03	1		
Grass CP3	G	0.01	1		
Juncus spp.	G			0.07	12
Luzula parviflora	G			0.69	4
Poa palustris	G	0.01	1	0.16	8
Trisetum spicatum	G			0.01	1
Lonicera involucrata	S			0.03	1
Ribes lacustre	S			0.49	4
Vaccinium myrtillus	S	47.49	99	24.95	94

Table 5.5 (continued)

Species	Life Form	Stand TL Cover	Stand TL Freq.	Stand LP Cover	Stand LP Freq.
Achillea lanulosa	F	0.01	1	0.04	7
Aquilegia elegantula	F	0.03	5	0.77	8
Arnica cordifolia	F	13.79	99	8.30	74
Arnica parryi	F			0.19	3
Calypso bulbosa	F	0.01	1	0.06	2
Chamerion angustifolium	F	0.46	32	6.50	72
Cirsium spp.	F			0.45	9
Drymocallis fissa	F			0.01	1
Erigeron eximius	F	1.65	20	2.25	50
Fragaria spp.	F	0.03	6	1.10	35
Galium triflorum	F			0.03	1
Geranium richardsonnii	F	0.24	7	4.80	44
Lathyrus leucanthus	F	2.85	34	8.17	67
Ligusticum filicinum	F			0.03	1
Lycopodium annotinum	F	0.01	4		
Mertensia ciliata	F	0.31	2	3.30	5
Mitella stauropetala	F	0.06	2	0.07	3
Moneses uniflora	F			0.11	6
Oreochrysum parryi	F	0.24	17		
Osmorhiza depauperata	F	0.16	13	0.21	22
Pedicularis racemosa	F	2.53	41	0.41	11
Polemonium pulcherrimum	F	0.16	2	0.01	2
Pseudocymopteris montanus	F			0.03	1
Pyrola asarifolia	F	0.69	8		
Ramischia secunda	F	0.24	7	0.38	15
Smilacina stellata	F			0.58	10
Streptopus amplexifolius	F			0.39	2
Taraxacum officinale	F			0.03	5
Unknown b.	F			1.53	15
Unknown d.	F			0.16	1
Unknown e.	F	0.03	1		
Viola adunca	F			0.01	1
Viola canadensis	F			0.39	27
Bromopsis canadensis	G			4.08	60
Carex foenea	G	0.04	7		
Carex geyeri	G			0.03	1
Carex rossii	G	0.02	1	4.64	44
Grass TL2	G	0.08	11		
Grass TL4	G	0.04	3		
Luzula parviflora	G	0.04	2		
Linnaea borealis	S	1.43	21		
Lonicera involucrata	S			0.32	4
Mahonia repens	S	0.06	6		
Paxistima myrsinites	S	0.97	44	0.58	15
Ribes lacustre	S			0.25	5
Ribes montigenum	S			0.22	3
Rosa spp.	S	0.02	3		
Sambucus racemosa	S	0.01	1	0.03	1
Vaccinium myrtillus	S	4.05	55	1.40	24
Vaccinium scoparium	S	15.09	67	4.70	36

Grand Mesa Stands

Understory structure and composition are quite different in stands CW and BC. In stand CW, richness and cover values are low, similar to those for stands HB and HC (Tables 5.4 & 5.6). This is probably the result of high elevation, low diffuse light, and a well-drained, cobbly substrate. The shrub Vaccinium accounts for 64% of the total cover (Table 5.5). Several species present indicate cool, locally moist conditions in this stand.

In contrast, BC is a mesic stand 200 m lower in elevation. Understory cover and richness are high (Tables 5.4 & 5.6). Non-vascular plant cover in BC is also high. Several of the plots have total understory cover well over 70%. Nearly 65% of the total cover is composed of forbs (Table 5.5). Of the shrub cover, V. myrtillus comprises 83%.

Comments

Based on these results in understory structure and composition, it is apparent that the drier stands (HC, CP, RC, CW, and WC) have understories dominated by Vaccinium spp. (Fig. 5.1). In the more mesic stands, especially LP, BC and BL, and to a lesser extent TL, forbs become dominant or nearly equal (by cover) with the shrub component. These characteristics must be

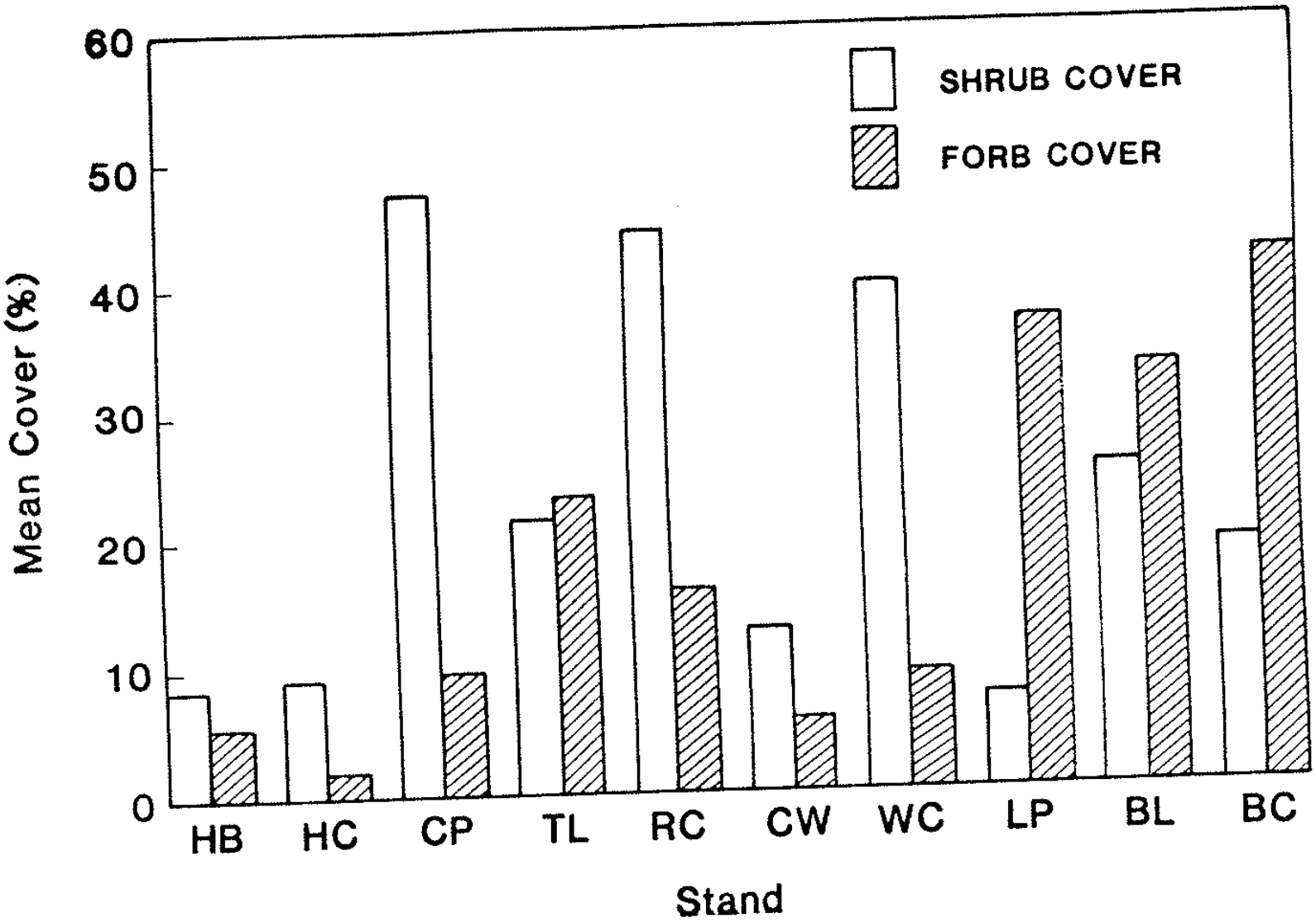

Figure 5.1. Mean shrub and forb cover (%) in the ten stands. Stands are subjectively ranked, based on elevation and topographic position, from xeric (HB & HC) to mesic (BL & BC). The apparent trend is a shift from dominance of shrubs to dominance of forbs.

considered when examining the response of the understory to disturbance.

Similarity Indices

In looking at pairwise comparisons of similarity indices between stands, the most obvious pattern corresponds with the understory structure, as discussed above. Soil moisture conditions are important indetermining species richness and abundance, and this is evident in the similarity indices. Similarity by species abundance shows the strongest differentiation between groups of stands. The xeric stands, HB and HC, are most similar to each other both in terms of richness and species abundance (Table 5.7). This is also related to their geographic proximity and common stand history. They are dissimilar to all the other stands, especially by species abundance.

Stands BC and BL are similar in richness and abundance due to their mesic conditions (Table 5.7). Yet stands CP and RC have the highest similarity, by abundance, of any of the stands. This is the result of the strong dominance by Vaccinium in these stands. Stand WC is also dominated by Vaccinium and has a high similarity with stand RC, yet is not so similar with CP. There are somewhat different forb components in the two stands. Stand LP has low similarities, by abundance,

Table 5.7. Sorenson's index of similarity (%) and community coefficient (%) between each pair of stands. The index of similarity is based on the number of species in common to the pair of stands. The community coefficient is based on the abundance of species in common to the pair of stands.

Index of Similarity

Stands	HB	HC	CP	BL	TL	LP	RC	WC	CW	BC
HB	100	63.7	27.6	22.5	47.1	30.0	27.3	23.3	30.8	26.5
HC		100	22.5	14.3	34.0	25.0	25.0	20.5	22.9	18.8
CP			100	55.2	38.8	42.1	53.3	33.9	29.1	38.1
BL				100	32.5	42.7	41.1	36.1	38.2	59.8
TL					100	58.0	49.1	46.2	45.8	39.0
LP						100	58.1	42.6	49.1	53.5
RC							100	53.3	53.7	54.3
WC								100	40.0	52.2
CW									100	49.2
BC										100

Community Coefficient

Stands	HB	HC	CP	BL	TL	LP	RC	WC	CW	BC
HB	100	47.0	15.7	16.1	18.5	21.3	14.1	15.2	29.3	14.1
HC		100	13.2	12.0	14.9	9.6	11.4	12.4	26.6	11.0
CP			100	55.5	17.6	13.6	81.5	33.9	29.1	38.1
BL				100	31.8	27.3	58.2	36.1	38.2	59.8
TL					100	42.6	27.6	33.8	25.3	36.0
LP						100	18.6	19.5	15.2	32.6
RC							100	66.2	45.5	49.1
WC								100	40.0	52.2
CW									100	49.2
BC										100

with stands RC, WC, CW and CP. This is due to the dominance of forbs in LP versus Vaccinium in the others. Stands CW and CP are also dissimilar with stand TL, again because of their dominance by Vaccinium.

Similarity measured by richness shows that eight of these subalpine stands have somewhat similar floras (Table 5.7). Stands HB and HC are the exceptions to this, due to their xeric nature.

Tree Seedling and Sapling Densities

Seedling densities indicate much variability in regeneration patterns corresponding to stand age, disturbance severity and soil moisture conditions. Fir seedlings are significantly more abundant than spruce (Mann-Whitney U statistic, $P \leq 0.05$) in all stands (Table 5.8), except stands HC and LP. Fir sapling densities are significantly more abundant than spruce in all stands (Mann-Whitney U, $P \leq 0.05$), except stand LP, where there is no statistical difference (Table 5.9). The greater abundance of fir seedlings and saplings in subalpine forests is typical of old-growth spruce-fir stands (Veblen 1986a).

Of the four stands with lodgepole present, only HB shows any recent recruitment. Lodgepole saplings are present in HB and HC in low numbers, but TL and CP have no saplings of this seral species.

Table 5.8. Tree seedling (<1.4 m tall) densities (no./ha.) and the percent of seedlings established on logs in the ten sampled stands. Short seedlings = <20 cm tall. Tall seedlings = 20-140 cm tall.

	Abies lasiocarpa			*Picea engelmannii*			*Pinus contorta*	
Stand	Short	Tall	% On Logs	Short	Tall	% On Logs	Short	Tall
HB	300	1100					200	400
HC	200	100		100			100	
CP	800	2700		100	300			
BL	2500	5400	22	2500	1800	65 **		
TL	14600	6700		600	2800			100
LP	1800	700	16	1300	600	37 *		
RC	1300	5100	3	600	3100	16 **		
WC	7100	5000	45	3400	1100	82 **		
CW	900	2100	13	200		100 *[1]		
BC	1400	1600	10	200	500	29		

* Significantly more spruce than fir on logs at $P \leq 0.05$.
** Significantly more spruce than fir on logs at $P \leq 0.01$.
[1] This stand has only 2 spruce seedlings, both on logs.

Table 5.9. Tree sapling (>1.4 m tall but <4 cm DBH) densities in the ten sampled stands.

Stand	Abies lasiocarpa	Picea engelmannii	Pinus contorta	Total
HB	210	13	48	271
HC	122		4	126
CP	1175	144		1319
BL	1179	443		1622
TL	936	505		1441
LP	525	225		750
RC	1270	470		1740
WC	895	205		1100
CW	330	65		395
BC	527	109		636

Stands HB and HC have low numbers of seedlings (Table 5.8). However, HB does show a slight increase in fir and lodgepole seedlings, implying new recruitment following the blowdown. Low numbers of seedlings in stands CW, CP, and BL (Table 5.8) may be attributed to a relative lack of bare mineral soil in combination with low light levels. Stands TL, RC, WC, and BL exhibit abundant seedlings and saplings of both spruce and fir (Tables 5.8 & 5.9).

Age data for short seedlings (< 20 cm height) of all species indicate that there was establishment of both spruce and fir following the 1973 blowdown or 1940s outbreak (Veblen et al. 1989a, 1989b).

The six stands lacking lodgepole pine have some seedlings of both fir and spruce established on logs (Table 5.8), in all cases more spruce than fir. Only in four cases is this difference statistically significant.

Stands WC and BL have significantly higher percentages of spruce seedlings on logs (at $P \leq 0.01$) than stands LP, BC and RC. Stand CW is not considered because only 2 spruce seedlings were found, both on logs. As with spruce seedlings, stand WC has significantly more ($P \leq 0.01$) fir seedlings established on logs than the other five stands (Table 5.8). RC has significantly fewer ($P \leq 0.01$) than any of the other stands.

The two stands with high percentages of seedlings on logs, WC and BL, also have the highest cover of non-vascular plants among these six stands (Table 5.4). RC, with the lowest percentage of seedlings on logs, also has the lowest cover of non-vascular plants. These results suggest that the more mesic the stand, the more likely it is that seedlings of both spruce and fir will establish on logs. Logs in these stands are less likely to become desiccated and therefore are good sites for the growth of seedlings.

Within Stand Correlations

Results from the Spearman Rank Correlations indicate that the response of the understory to disturbance in the canopy is complex and variable. In general, cover increases in the more severely disturbed stands and richness appears to decline in stands with higher live basal areas.

Relationships between Understory Cover and Richness and the Canopy

Hidden Valley Blowdown: Stand HB. In this stand, understory cover appears to respond negatively to the presence of live trees. Graminoid and total cover are less where live fir or spruce are greater (Table 5.10). In contrast, forb cover is positively correlated with dead fir. Total richness and herb richness show a similar, inverse relationship with live fir (Table 5.11). Non-vascular plants (mosses and lichens) are associated with spruce (Table 5.10), as a result oftheir joint occurrence at more moist sites.

Hidden Valley Control: Stand HC. In this stand, understory cover and richness primarily respond to variations in soil moisture, rather than to the canopy. Forb and total cover, non-vascular plant cover, and total and shrub richness are all positively correlated with live fir (Table 5.10). In this xeric stand, dominated by lodgepole pine, the correspondence of mosses and lichens with live fir may indicate more mesic locations within the stand, and therefore locations more conducive to understory growth. There is also a positive correlation between dead spruce and forb cover and shrub richness (Table 5.11). Dead spruce make up < 1% of the dead-standing basal area (Table 3.3). The

Table 5.10. Spearman rank correlations for understory cover, by life-form, with basal areas of live and dead-standing trees, by species. Correlations between .56 and .75, or -.56 and -.75, are significant at the 0.05 level. Correlations $\geq$ .75 (or $\leq$ -.75) are significant at the 0.01 level. See Chapter IV (Methods) for key of variable abbreviations.

Variable Pair	Stands .HB	.HC	.TL	.LP	.RC	.WC	.CW	.BC	.CP	.BL
SHRBCVR										
x LvA							.782			
x LvE				-.624				-.588		
x DdA								.721	.624	
x LvTTL							.636			
x DdTTL								.612		
FRBCVR										
x LvA		.706			-.624	-.588				
x DdA	.585		.673					.697		
x DdE		.579	.746							
x DwlE				-.564				-.588		
x DdTTL			.564					.624		
x DwlTTL						.709				.661
GRMCVR										
x LvE	-.809					-.624	.709			
x LvTTL						-.697				
x DdA										.846
x DdTTL			.685							
TTLCVR										
x LvA	-.818	.770			-.697					
x LvE			-.842							
x DdA								.794	.576	
x DwlA									.600	
x DdE			.746			.758				
x DwlE				-.588				-.600		
x LvTTL					-.567					.612
x DdTTL						.746		.709		
x DwlTTL						.673				.673
NONVCVR										
x LvA		.794	-.746		.564					
x LvE	.682		-.758							-.585
x DdA	.694	.576								
x DdE	.724		.770			.661				
x DwlE						.688			.782	
x DdC			-.649							
x LvTTL			-.758		.603		.609		-.612	

Table 5.11. Spearman rank correlations for understory richness, by life-form, with basal areas of live and dead-standing trees, by species. See Table 5.10 for levels of significance.

Variable Pair	Stands .HB	.HC	.TL	.LP	.RC	.WC	.CW	.BC	.CP	.BL
RCHNES										
x LvA	-.661	.582			-.621					
x LvC			-.567							
x LvTTL	-.309[1]	.267[1]	-.573	-.294[1]	-.649	-.479[1]	-.406[1]	-.212[1]	-.003[1]	-.067
x DwlTTL						.776				
SHRBSPP										
x LvA		.730	.624	.603						
x LvE				-.579						
x LvC			.606							
x DdE		.591				.636				
x DdC			.806							
x LvTTL			.703							
x DdTTL						.673		.576		
x DwlTTL			.655							
HERBSPP										
x LvA	-.576				-.697					
x LvC			-.585							
x LvTTL			-.627							
x DwlTTL						.697				

[1] Denotes correlations that are not statistically significant, but are shown to illustrate a possible trend.

presence of spruce, live or dead, probably signals more mesic locations within the stand, rather than being a direct cause of understory variation.

The correlations within the understory of stand HC imply better establishment and growth of understory plants in more mesic areas in the stand. Forb cover, total richness and shrub richness are all positively correlated with cover of non-vascular plants (Table 5.12).

Control Stands (Spruce Beetle)

Cameron Pass: Stands CP & BL. Both of these stands show a relationship between the canopy andvariation in the understory. In stand CP, where the understory is dominated by Vaccinium, both shrub and total cover are positively correlated with dead fir (Table 5.10). The high cover of Vaccinium in this stand may therefore be a result of both its response to the death of fir trees and to the xeric nature of the stand.

In stand BL, forb, graminoid and total cover respond positively to the death of trees (Table 5.10). Shrub cover has strong negative correlations with herbaceous cover and with total richness and herbaceous richness (Table 5.12). This indicates that areas of high shrub cover have lower herbaceous richness.

For both stands CP and BL, understory richness

Table 5.12. Spearman rank correlations between understory cover and richness, by life-forms. See Table 5.10 for levels of significance.

Variable Pair	Stands .HB	.HC	.TL	.LP	.RC	.WC	.CW	.BC	.CP	.BL
SHRBCVR										
x FRBCVR										-.733
x GRMCVR				.612						-.709
x NONVCVR				.782			.670			.600
FRBCVR										
x GRMCVR				.576						
x NONVCVR		.730								
TTLCVR										
x SHRBCVR	.782	.830		.552			.697	.636	.903	
x FRBCVR		.573	.588	.867	.600		.673	.952	.673	
x GRMCVR				.855		.564				
x NONVCVR			.697			.624	.615			
RCHNES										
x SHRBCVR		.564		.876						-.909
x FRBCVR	.564				.609	.939	.806	.788	.870	.788
x GRMCVR		.715		.652						.642
x TTLCVR	.849	.667		.706			.582	.667		
x NONVCVR		.600		.815						-.576
SHRBSPP										
x SHRBCVR				.676						
x FRBCVR								.661		
x GRMCVR		.576								
x TTLCVR	.609	.573						.576		
x NONVCVR		.682		.785						
HRBSPP										
x SHRBCVR	.539[1]	.576	-.536[1]	.491[1]	-.115[1]	-.527[1]	-.003[1]	-.206[1]	-.367[1]	-.891
x FRBCVR	.703			.600	.733	.903	.839	.703	.870	.818
x GRMCVR		.646		.594						.624
x TTLCVR	.806			.661			.633	.594		
x NONVCVR					-.588					-.576

[1] Denotes correlations that are not statistically significant, but are shown to illustrate a possible trend.

is not significantly correlated with the canopy. However, both stands have a slightly negative correlation between richness and total live basal area (Table 5.11), indicating that the canopy may be influencing the number of species occurring in these stands.

Spruce Beetle-Disturbed Stands

White River: Stands TL, LP & RC. In stand TL, understory variation indicates a strong response to the death of spruce and lodgepole (Table 5.10). Forb, graminoid and total cover are all positively correlated with either dead spruce or total dead basal area. This implies an increase in understory cover in areas of increased canopy mortality.

Stand LP shows few interactions between the canopy and the understory. Shrub cover is negatively correlated with live spruce, while forb and total cover are negatively correlated with dead-with-logs spruce (Table 5.10). These results suggest that shrubs have increased in abundance in areas of fewer live spruce. In contrast, forbs and graminoids decrease in abundance in areas of more dead spruce.

In stand RC, which is dominated by Vaccinium, understory cover is related primarily to the basal area of live fir (Table 5.10). Forb and total cover decrease

in areas of more live fir. These results indicate that in this dense stand, any increase in live fir trees results in a decrease of understory cover.

In all three of these stands, total understory richness, dominated by herbs, is negatively correlated with basal area of live trees (Table 5.11). In LP, shrub richness has a negative relationship with live spruce and a positive one with live fir. Fir and shrubs may occur together in drier sites, while spruce occupies slightly moister locations. In RC, the negative correlation between herbaceous richness and live fir may similarly reflect moisture gradients.

In stand TL, the number of shrub species is positively correlated with both live and dead basal areas. This seeming contradiction can possibly be explained by the presence of shrubs typical of both cool, moist forests (Linnaea and Paxistima) and those found in drier forests (Mahonia and Sambucus). This stand with its north aspect but high diffuse light (Table 5.3), may provide both conditions, resulting in the presence of shrub species in two distinct types of microsites.

Within the understory, stand LP has many significant positive correlations between different elements of the understory (Table 5.12). These strong associations suggest that in more mesic locations in the

stand, cover and richness increase. They also imply a patchy understory, consistent with the somewhat mesic conditions of the stand and the patchy nature of the canopy.

In both stands TL and RC, there is a negative correlation between shrub cover and herbaceous species (Table 5.12), suggesting that areas with high shrub cover have fewer herbaceous species.

Rabbit Ears Pass: Stand WC. The understory in this stand shows a strong response to changes in the canopy, both in cover and richness. Forb and graminoid cover decrease in areas of higher live basal area (Table 5.10). Forb cover and total cover are positively correlated with dead-standing basal areas. Understory richness is similarly related, having a slightly negative relationship with live basal area and a positive relationship with dead basal area (Table 5.11). These results indicate that the death of canopy spruce leads to an increase in both cover and richness for all life-forms in the understory.

Within the understory, shrub cover and herbaceous richness have a slightly negative relationship (Table 5.12).

Grand Mesa: Stands CW & BC. These two stands show contrasting responses of the understory to the canopy. In stand CW, shrub cover and graminoid cover are positively correlated with basal area of live trees (Table 5.10). In this rocky, high elevation stand, both trees and the understory plants may be establishing in less rocky locations where more soil has developed and soil moisture is higher.

In stand BC shrub, forb and total understory cover are positively correlated with dead fir and total dead basal area (Table 5.10). These results indicate a definite increase in understory cover in response to the death of fir trees, which account for > 80% of the dead-standing basal area and density (Table 3.3).

Richness follows the trend seen in previously discussed stands, being slightly negatively correlated with total live basal area in both CW and BC (Table 5.11). In stand BC, shrub richness is positively correlated with total dead basal area, indicating an increase in shrub species in the vicinity of dead trees.

Both of these stands have many positive correlations between cover and richness (Table 5.12). Of particular interest in CW is the relationship of shrub and total cover with cover of non-vascular plants, indicating greater understory cover in moist areas.

Relationships Between Seedling and Sapling Densities and the Canopy or Understory

There are few trends in the results for fir seedling densities. In stands BC and CP, seedlings are positively correlated with dead basal area, especially that of fir (Table 5.13). This suggests an increased establishment of fir seedlings in the vicinity of dead fir, consistent for these stands in which fir comprises the major portion of dead-standing basal area and diffuse light is low (Table 5.3). Due to the low densities of spruce seedlings, there are no significant correlations between spruce seedlings and the canopy. In stands TL, BC and CP, spruce saplings are negatively correlated with live fir or spruce (Table 5.13). In stands HB, HC, TL and WC, saplings are positively correlated with dead-standing basal area (Table 5.13). These results indicate an increase in sapling densities in the vicinity of dead-standing trees in these stands.

There are few trends apparent in the results of the correlations between seedlings and the understory. The first is the positive correlation between fir seedlings and understory cover and richness in stand CW (Table 5.14). In this stand, the understory and the canopy apparently occur in less rocky, more mesic microsites within the stand. The correlations between fir seedlings and the understory suggest that the same

Table 5.13. Spearman rank correlations for seedling and sapling densities, by species, with basal areas of live and dead-standing trees, by species. See Table 5.10 for levels of significance.

Variable Pair	Stands .HB	.HC	.TL	.LP	.RC	.WC	.CW	.BC	.CP	.BL
ASEEDS										
x LvA	.670				.564					
x LvE			-.649					-.773		
x LvC			.649							
x DdA						-.597		.585	.564	
x DwlA									.655	
x LvTTL	.573				.642					
x DdTTL								.779		
x DwlTTL									.570	
ASEEDS										
x ESEEDS			.842	.721		.627				
ESEEDS: there are no significant correlations between spruce seedlings and the canopy.										
ASAPS										
x LvE	.767									
x DdA	.733	.652				-.630				
x DwlA			.667							
x DdE	.673	.591					-.761			
x DwlE										-.573
x DdC			-.606							
x DwlC		.846								
x LvTTL	.927									
x DdTTL	.612	.561							-.633	
x DwlTTL	.670	.846							-.615	
ESAPS										
x LvA			-.812					-.573		
x LvE	.694				.830				-.718	
x LvC									.627	
x DdA	.755			-.621						
x DwlA						.603				
x DdE	.642			-.664						
x DwlE			.697							
x DdC			-.873							
x LvTTL	.570		-.879							
x DdTTL				-.749					-.603	
x DwlTTL									-.579	
ASAPS										
x ESAPS	.570		.621				.867	.827	.861	

Table 5.14. Spearman rank correlations of seedling and sapling densities, by species, with understory cover and richness, by life-form. See Table 5.10 for levels of significance.

Variable Pair	Stands .HB	.HC	.TL	.LP	.RC	.WC	.CW	.BC	.CP	.BL
ASEEDS										
x SHRBCVR								.609		
x FRBCVR							.603			
x TTLCVR			.576				.706			
x RCHNES							.670			
x SHRBSPP				.606						
x HRBSPP							.691			
x LTRCVR									.588	
x RKINES								.703		
ESEEDS										
x SHRBCVR										-.864
x RCHNES										.758
x SHRBSPP					.615					
x HRBSPP										.688
ASAPS										
x FRBCVR									.664	
x GRMCVR										.573
x RCHNES									.800	
x SHRBSPP				.730						
x LTRCVR		.797								
x RKINES	-.664		-.655							
ESAPS										
x FRBCVR									.773	
x GRMCVR				-.609						
x NONVCVR	.749		.703					.621		
x RCHNES									.703	

may be true for the establishment of seedlings. In stand BL, the negative correlation between spruce seedlings and shrub cover probably reflects the establishment of shrubs in drier microsites versus wetter sites for spruce seedling establishment (Table 5.14).

There are few trends in the results between saplings and the understory. The most consistent is the positive correlation between spruce saplings and cover of non-vascular plants in stands HB, TL, and BC (Table 5.14). This suggests that the density of spruce saplings is greater in more mesic locations in these stands.

Correlations for all Stands Combined

The results for the correlations of the combined data for all stands show that many of the trends are similar to those seen within stands. However, the addition of the diffuse site factor to the data set allows additional interpretation.

Relationships Between the Canopy and the Understory

Results of correlations between the diffuse site factor and the canopy show that live spruce and the diffuse site factor are negatively correlated ($r = -.794$). There is a weak positive correlation between

total dead basal area and the diffuse site factor (r = .249).

In general, forb, graminoid and total understory cover are positively correlated with dead-standing basal areas (Table 5.15). All strata of the understory have negative correlations between cover and the diffuse site factor, although none are statistically significant. Thus, understory cover increases with an increase in dead trees, but an increase in diffuse light may lead to a decrease in cover. This suggests that light may not be the controlling factor for understory cover, rather it is competition with the canopy for soil nutrients or moisture.

In contrast, the results for species richness show different relationships for the different strata. Total richness is positively correlated with total dead-with-logs basal area and is negatively correlated with total live basal area and the diffuse site factor (Table 5.15). Herbaceous richness is also negatively correlated with the diffuse site factor. These results are similar to those seen above for cover and the diffuse site factor. However, shrub richness is negatively correlated with live basal area and positively correlated with both dead-with-logs basal area and the diffuse site factor. This suggests that more dead-standing trees and therefore more diffuse

Table 5.15. Spearman rank correlations between canopy variables and understory variables, for all stands combined. See Table 5.10 for levels of significance.

Canopy Variables	.LvA	.LvE	.DdA	.DwlA	.DdE	.DwlE	.LvTTL	.DdTTL	.DwlTTL	.DFFSE
Understory Variables										
SHRBCVR										-.346[1]
FRBCVR			.576			.664		.685	.733	-.333[1]
GRMCVR					.855	.736				-.152[1]
TTLCVR	.576		.685	.746						-.442[1]
NONVCVR				.649						-.527[1]
RCHNES							-.212		.576	-.455[1]
SHRBSPP		-.576					-.649		.673	.612
HERBSPP	.750									-.621
ASEEDS										-.136[1]
ASAPS										-.249[1]
ESEEDS	.588				.733	.700		.600		-.224[1]
ESAPS					.673	.785		.770	.612	
ASDSOL	.570	.558[1]		.624	.642					-.424[1]
ESDSOL	.594	.679	.606	.685						-.436[1]

[1] Denotes correlations that are not statistically significant, but are shown to illustrate a possible trend.

light may result in an increase in the number of shrub species. This reflects the tendency for shrubs to dominate more open, relatively xeric stands.

Relationships Between the Canopy and Seedlings and Saplings

Only spruce seedlings and saplings have any significant correlations with the canopy variables. Spruce seedling and sapling densities have positive relationships with dead-standing trees (Table 5.15). This suggests that spruce seedling and sapling establishment is better in the stands with more dead-standing trees, especially dead spruce. As with understory cover, the slightly negative correlations between seedling or sapling densities and the diffuse site factor, suggest the importance of competition for soil resources.

Spruce and fir seedlings on logs have positive correlations with live spruce and fir, and also with dead spruce or fir (Table 5.15). Further, seedlings on logs have slightly negative correlations with the diffuse site factor. Together, these results imply that wetter stands with higher basal areas have less diffuse light, and therefore more mesic microsites on logs. Thus, seedlings are more likely to survive on logs than in drier stands, where log microsites are subject to desiccation.

Relationships Within the Understory

Seedling and sapling densities have strong positive correlations between the two species, suggesting that stands favorable to the regeneration of fir are also favorable to spruce regeneration (Table 5.16). Stands with more spruce seedlings on logs also have more fir seedlings on logs.

Strata within the understory show definite patterns of relationships with seedlings and saplings. Shrub cover has a positive association with fir, possibly a result of their better establishment and growth in slightly drier locations (Table 5.16). In contrast, forb and graminoid cover are positively associated with spruce seedlings or saplings. This supports the conclusion that herbaceous plants are more abundant in more mesic locations, as are spruce seedlings and saplings. Non-vascular plant cover is positively correlated with both fir and spruce seedlings, implying that seedlings establish better in moister locations.

Seedlings on logs are positively correlated with both graminoid and non-vascular plant cover (Table 5.16). This supports the previous interpretation that the more mesic stands have more seedlings of both species established on logs. Also, it suggests that graminoid cover may be higher in the more mesic stands.

Table 5.16. Spearman rank correlations between understory variables, for all stands combined. See Table 5.10 for levels of significance.

	.ASEEDS	.ESEEDS	.ASAPS	.ESAPS	.ASDSOL	.ESDSOL	.RCHNES	.LTRCVR	.RKINES
ASEEDS1.000	.821	.785	.803						-.633
ESEEDS	1.00	.746	.806	.667				.673	-.891
ASAPS		1.000	.818				.576	.636	-.564
ESAPS			1.000						-.770
ASDSOL				1.000	.927			.612	-.570
ESDSOL					1.000			.503[1]	-.375[1]
RCHNES						1.000		.636	
LTRCVR								1.00	
RKINES									1.00
SHRBCVR.718			.830						
FRBCVR				.624			.891	.721	-.564
GRMCVR	.612				.830	.649		.624	-.685
TTLCVR	.649	.830	.576				.685	.927	
NONVCVR.700	.721				.739	.667			-.576
SHRBSPP									
HRBSPP			.658				.949		

[1] Denotes correlations that are not statistically significant, but are shown to illustrate a possible trend.

The positive correlation of seedlings on logs and litter cover reflects the higher plant productivity of the more mesic stands.

The negative correlations between percent rockiness and many of the understory variables (Table 5.16) confirms that the more xeric stands, which tend to be rockier, have less understory growth.

CHAPTER VI

DISCUSSION AND CONCLUSIONS

Understory Structure and Composition

Generally, the results of this investigation show that the determinants of the distribution of understory vegetation are a complex of interacting environmental factors. The response of the understory in these ten stands to disturbance of the canopy appears to be related to soil moisture and nutrients, elevation, light and disturbance severity. However, it must also be considered that the patterns of understory structure and composition seen in this study are changing over time. The initial response of the vegetation to the disturbance events is probably still a component of the patterns, but cannot be separated from them by the methods used.

The broad patterns of understory structure and composition may be largely controlled by soil moisture conditions in the stands investigated. Evidence for this is in the dominance of the drier stands by *Vaccinium* spp. The relatively mesic stands are dominated by herbaceous plants. Species richness also

corresponds closely with moisture conditions, as shown by the lower values for the drier stands (HB, HC, RC and CW) and higher values for the more mesic (LP, BC and BL). In all the stands, total richness was largely determined by herbaceous richness.

In conifer forests, herbaceous plants may be more sensitive indicators of site conditions than trees (Rowe 1956, Whittaker 1962, Mueller-Dombois 1964, Peet 1981). Peet (1978, 1981) has demonstrated that the relationship of diversity with moisture in Colorado Front Range forests changes with elevation and generalizations cannot be made outside of the context of this changing relationship. Del Moral (1972) found a similar interaction of diversity, elevation and moisture in the Pacific Northwest, where soil moisture was primarily controlled by the presence or absence of serpentine-derived soils. The lower understory richness in stands RC and CW may be a result of this interaction between moisture and elevation in influencing species richness.

The hypothesis of an increase in cover with an increase in disturbance severity is supported by the correlation results. Many of the stands show a positive correlation between understory cover and basal area of dead-standing trees. The combined data from the ten stands also show an increase in understory cover with an

increase in dead-standing trees. These results strongly suggest that an increase in disturbance severity, as measured by percent dead-standing basal area, results in an increase in understory cover. However, all strata of the understory show an inverse relationship between cover and diffuse light. This suggests that the release of soil resources by the death of the competitively dominant trees is more important to understory abundance and composition than light.

Species richness may vary independently for different strata or life-forms within a plant community (Whittaker 1960, Auclair and Goff 1971, Glenn-Lewin 1977, Peet 1978). This is supported by the results of this study. The prediction that increased disturbance severity will result in increased diversity is also supported. Furthermore, the relative importance of the shrub versus herbaceous strata may be affected by disturbance severity. Total and herbaceous richness tend to be higher in patches with higher mortality of trees, yet are lower in patches with higher diffuse light. Shrub species are apparently favored by increased mortality of the dominant trees and by an increase in diffuse light. The more severely disturbed patches, with larger gaps in the canopy and increased diffuse light, may therefore show an increase in the number of shrub species as compared to herbs. Both the

within stand results and results for the combined data support these trends.

The mechanism for the response of these two strata may be related to differing requirements for soil nutrients and moisture or light. In addition to increasing light with increasing gap size, soil and air temperatures change (Collins et al. 1985). Larger gaps have higher maximum and lower minimum soil temperatures. Air temperature depends more on gap orientation, insolation and wind directions, but appears to fluctuate more in gaps than beneath intact canopy (Collins et al. 1985). Soil moisture conditions will also differ in gaps. In this study, the presence of larger gaps (as indicated by higher diffuse light) in the more disturbed patches may be favorable to the establishment and growth of shrub species as compared to herbaceous species. The greater extremes of air and soil temperatures in these gaps may be detrimental to herbaceous plants.

These trends are similar to those found by Davison and Forman (1982), Huenneke (1983) and Moore and Vankat (1986), wherein the cover of herbaceous or shrub plants increased with gap formation, but herbaceous richness was observed to decrease or remain the same. Physiological studies by Smith (1981) demonstrated that midday wilting is common in several subalpine understory species that are exposed to sunflecks of varying

duration in conifer forests, especially non-evergreen, shallow-rooted forbs. The capability of two species of Arnica to withstand this midday wilting is different (Young and Smith 1979), and their small-scale distribution is related to their water relations in response to sunfleck duration. The increase in diffuse light seen in the more severely disturbed stands of this study is almost certainly accompanied by an increase in the amount of direct light (i.e. sunflecks) and perhaps by a change in the species able to withstand the increased solar radiation and water stress.

Interactions within the understory community can also be determinants of community structure. Whittaker (1960) suggests that shrub cover is the major influence upon small-scale distributions of herbaceous plants. Wilson (1988) demonstrated that shrubs increased shading, soil moisture and litter depth and decreased soil temperature. In this study, 7 out of 10 stands have an inverse relationship between shrub cover and herbaceous richness, indicating that increased shrub cover may decrease herbaceous richness. Alternatively, this relationship may result from the differing requirements of shrubs and herbs for soil moisture or from a differing response the competitive influence of the canopy.

Spruce and Fir Regeneration

Some of the more severely disturbed stands in this study have abundant regeneration of both spruce and fir (TL and RC), supporting the hypothesis of increased tree seedling numbers. Age data for short seedlings in the disturbed stands show that short seedlings are less than 40 years of age (Veblen et al. 1989a, 1989b). The results of the within stand correlations provide additional evidence for increased regeneration of spruce and fir following disturbance. Several stands (HB, TL and WC) have positive relationships between spruce or fir sapling densities and dead-standing trees. The combined data for all stands show a positive relationship between spruce seedling density and dead-standing trees. These results indicate an apparent increase in seedling or sapling densities with increased tree mortality due to severe disturbance.

This study provides quantitative evidence for the proposed better establishment of spruce on decaying wood (Smith 1954, Knapp and Smith 1982). Six of the ten stands investigated have spruce and fir seedlings established on logs; in four cases there are significantly more spruce than fir. Additionally, the percentage of seedlings on logs was inversely related to diffuse light, suggesting that an increase in light

levels may cause more rapid drying of these log microsites and lowered seedling survival.

Conclusions

The results of this study generally support the original hypotheses and predictions concerning understory structure and composition. Moisture conditions appear to control the broad patterns of understory structure and composition, but richness and cover both tend to be higher in the more severely disturbed stands in comparison with old-growth stands. Analyzing the results for the different strata of the communities in these patches allowed additional trends to be seen. In particular, it appears that shrub richness and forb richness respond differently to mortality of the tree stratum. The relase of soil nutrients and moisture may be more important to herbaceous species than shrubs, which appear to respond more to the release of light. This aspect of the small-scale distribution of understory plants in these types of forests deserves further attention.

Another interesting aspect emerging from this study is the possible influence of the shrub layer on the distribution of herbaceous plants. Lastly, these results support the prediction that there is increased tree establishment following severe beetle outbreaks in subalpine forests of the southern Rocky Mountains.

REFERENCES

Ahlgren, C.E. 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. Ecology 41:431-445.

Alaback, P.B. 1982. Forest community structural changes during secondary succession in southeast Alaska. Pp. 70-79 in Means, J.E. (ed.), Forest Succession and Stand Development Research in the Northwest. Forest Research Laboratory, Oregon State University, Corvallis.

Alaback, P.B. and Herman, F.R. 1988. Long-term response of understory vegetation to stand density in Picea-Tsuga forests. Canadian Journal of Forest Research 18:1522-1530.

Alexander, R.R. 1987. Ecology, silviculture, and management of Engelmann spruce-subalpine fir type in the central and southern Rocky Mountains. U.S. Department of Agriculture Forest Service Agriculture Handbook 659.

Anderson, M.C. 1964. Studies of the woodland light climate. I. The photographic computation of light conditions. Journal of Ecology 52:27-41.

Anderson, M.C. 1966. Some problems of simple characterization of the light climate in plant communities. Pp. 77-90 in Bainbridge, R., Evans, G.C., and Rackham, O. (eds.), Light as an Ecological Factor. Blackwell, Oxford.

Anderson, R.C., Loucks, O.L., and Swain, A.M. 1969. Herbaceous response to canopy cover, light intensity and throughfall precipitation in coniferous forests. Ecology 50:255-263.

Armour, C.D., Bunting, S.C., and Neuenschwander, L.F. 1984. Fire intensity effects on the understory in ponderosa pine forests. Journal of Range Management 37:44-49.

Auclair, A.N. and Goff, F.G. 1971. Diversity relations of upland forests in the western Great Lakes area. American Naturalist 105:499-528.

Auerbach, M. and Shmida A., 1987. Spatial scale and the determinants of plant species richness. Trends in Evolution and Ecology 8:238-242.

Baker, F.S. 1944. Mountain climates of the western United States. Ecological Monographs 14:223-254.

Barry, R.G. 1972. Climatic environment of the east slope of the Colorado Front Range. Institute of Arctic and Alpine Research, University of Colorado, Occassional Paper 3.

Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology 65:1406-1419.

Bratton, S.P. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. American Naturalist 110:679-693.

Brewer, R. 1980. A half-century of changes in the herb layer of a climax deciduous forest in Michigan. Journal of Ecology 68:823-832.

Brokaw, N.V.L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. Biotropica 14:158-160.

Brokaw, N.V.L. 1983. Groundlayer dominance and apparent inhibition of tree regeneration by Aechmea magdalenae (Bromeliaceae) in a tropical forest. Tropical Ecology 24:194-200.

Canham, C.D. and Marks, P.L. 1985. The response of woody plants to disturbance: patterns of establishment and growth. Pp. 197-216 in S.T.A. Pickett and P.S. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Canham, C.D. and Loucks, O.L. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65:803-809.

Chazdon, R.L. 1988. Sunflecks and their importance to forest understorey plants. Advances in Ecological Research 18:1-63.

Chazdon, R.L. and Fetcher, N. 1984. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. Journal of Ecology 72:553-564.

Chronic, J. and Chronic, H. 1972. Prairie peak and plateau: A guide to the geology of Colorado. Colorado Geological Survey Bulletin 32.

Clements, F.E. 1910. The life history of lodgepole burn forests. U.S. Department of Agriculture Forest Service Bulletin 79.

Clements, F.E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institute of Washington Publication 242.

Collins, B.S., Dunne, K.P., and Pickett, S.T.A. 1985. Responses of forest herbs to canopy gaps. Pp. 217-234 in S.T.A. Pickett and P.S. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Cook, R.E. and Lyons, E.E. 1983. The biology of Viola fimbriatula in a natural disturbance. Ecology 64:654-660.

Crozier, C.R. and Boerner, R.E.J. 1984. Correlations of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. Oecologia 62:337-343.

Davison, S.E. and Forman, R.T.T. 1982. Herb and shrub dynamics in a mature oak forest: a thirty-year study. Bulletin of the Torrey Botanical Club 109:64-73.

del Moral, R. 1972. Diversity patterns in forest vegetation of the Wenatchee Mountains, Washington. Bulletin of the Torrey Botanical Club 99:57-64.

Denslow, J.S. 1980a. Gap partitioning among tropical rainforest trees. Biotropica 12:47-55.

Denslow, J.S. 1980b. Patterns of plant species diversity during succession under different disturbance regimes. Oecologia 46:18-21.

Denslow, J.S. 1985. Disturbance-mediated coexistence of species. Pp. 307-323 in S.T.A. Pickett and P.S. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Ehrenfeld, J.G. 1980. Understory response to canopy gaps of varying size in a mature oak forest. Bulletin of the Torrey Botanical Club 107:29-41.

Geiger, R. 1965. The Climate Near the Ground. Harvard University Press, Cambridge, Massachusetts.

Glenn-Lewin, D.C. 1977. Species diversity in North American temperate forests. Vegetatio 33:153-162.

Glidden, D.E. 1981. Summer wind studies near the Alpine Visitor's Center, Rocky Mountain National Park. Rocky Mountain Nature Assocciation, Inc., Estes Park, Colorado.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Review 52:107-145.

Hansen, W.R., Chronic, J., and Matelock, J. 1978. Climatography of the Front Range urban corridor and vicinity, Colorado. U.S. Geological Survey Professional Paper 1019.

Heinselman, M.L. 1970. The natural role of fire in northern conifer forests. Naturalist 21:14-23.

Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3:329-382.

Hess, K., and Wasser, C.H. 1987. Key to the Habitat Types of the White River-Arapaho National Forest, Colorado. U.S. Department of Agriculture Forest Service Publication, Rocky Mountain Region, Denver.

Hicks, D.J. 1980. Intrastand distribution patterns of southern Appalachian cove forest herbaceous species. American Midland Naturalist 104:209-223.

Huenneke, L.F. 1983. Understory response to gaps caused by the death of Ulmus americana in central New York. Bulletin of the Torrey Botanical Club 110:170-175.

Ives, R.I. 1938. Weather phenomena of the Colorado Rockies. Journal of the Franklin Institute 226:691-755.

Johnson, D.D. and Cline, A.J. 1965. Colorado mountain soils. Advances in Agronomy 17:233-281.

Knapp, A.K., and Smith, W.K. 1982. Factors influencing understory seedling establishment of Engelmann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa) in southeast Wyoming. Canadian Journal of Botany 60:2753-2761.

Knight, D.H., Rogers, B.S., and Kyte, C.R. 1977. Understory plant growth in relation to snow duration in Wyoming subalpine forest. Bulletin of the Torrey Botanical Club 104:314-319.

Loucks, O.L. 1970. Evolution of diversity, efficiency, and community stability. American Zoology 10:17-25.

Lovering, T.S. and Goddard, E.N. 1950. Geology and ore deposits of the Front Range, Colorado. U.S. Geological Survey Professional Paper 223.

Maguire, D.A. and Forman, R.T.T. 1983. Herb cover effects on tree seedling patterns in a mature hemlock-hardwood forest. Ecology 64:1367-1380.

Marks, P.L. 1974. The role of pin cherry (Prunus pensylvanica L.) in the maintenance of stability in northern hardwood ecosystems. Ecological Monographs 44:73-88.

Marr, J.W. 1961. Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Studies, Series in Biology 8.

Miles, J. 1979. Vegetation dynamics. Chapman-Hall, London.

Miller, P.C. 1964. Factors influencing the vegetation pattern on the White River Plateau in northwestern Colorado. Ph.D. Thesis, University of Colorado, Boulder.

Miller, P.C. 1970. Age distributions of spruce and fir in beetle-killed forests on the White River Plateau, Colorado. American Midland Naturalist 83:206-212.

Moir, W.H. 1966. Influence of ponderosa pine on herbaceous vegetation. Ecology 47:1045-1048.

Moore, M.R. and Vankat, J.L. 1986. Responses of the herb layer to the gap dynamics of a mature beech-maple forest. American Midland Naturalist 115:336-347.

Mueller-Dombois, D. 1964. The forest habitat types in southeastern Manitoba and their application to forest management. Canadian Journal of Botany 42:1417-1444.

Mueller-Dombois, D. and Ellenberg, H. 1974. Aims and Methods of Vegetation Ecology. Wiley, New York.

NH Analytical Software. 1985. Statistix: An Interactive Statistical Program for Microcomputers. NH Analytical Software, ST. Paul, Minnesota.

NOAA. 1971. Local climatological data: Annual summary with comparative data. U.S. Department of Commerce National Climatic Data Center, Asheville, North Carolina.

Oliver, C.D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management 3:153-168.

Oosting, H.J., and Reed, J.F. 1952. Virgin spruce-fir forest of the Medicine Bow Mountains, Wyoming. Ecological Monographs 22:69-91.

Peet, R.K. 1978. Forest vegetation of the Colorado Front Range: patterns of species diversity. Vegetatio 37:65-78.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. Vegetatio 45:3-75.

Peet, R.K. 1988. Forests of the Rocky Mountains. Pp. 63-101 in Barbour, M.G. and Billings, W.D. (eds.), North American Terrestrial Vegetation. Cambridge University Press, Cambridge.

Pickett, S.T.A. 1980. Non-equilibrium coexistence of plants. Bulletin of the Torrey Botanical Club 107:238-248.

Pickett, S.T.A. and Thompson, J.N. 1978. Patch dynamics and the design of nature reserves. Biological Conservation 13:27-37.

Pickett, S.T.A. and White, P.S. 1985. Patch dynamics: a synthesis. Pp. 371-384 in S.T.A. Pickett and P.S. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Putz, F.E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology 64:1069-1074.

Ramaley, F. 1907. Plant zones in the Rocky Mountains of Colorado. Science 26:642-643.

Rebertus, A.J., Williamson, B.G., and Moser, E.B. 1989. Fire induced changes in Quercus laevis spatial pattern in Florida sandhills. Journal of Ecology 77: (in press).

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 62:319-326.

Romme, W.H. and Knight, D.H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62:319-326.

Rowe, J.S. 1956. Uses of undergrowth plant species in forestry. Ecology 37:461-473.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63:1533-1546.

SAS Institute Inc. 1985. SAS User's Guide: Statistics, Version 5 Edition. SAS Institute Inc., Cary, North Carolina.

Schmid, J.M. and Frye, R.H. 1977. Spruce beetle in the Rockies. U.S. Department of Agriculture Forest Service General Technical Report RM-49.

Schmid, J.M. and Hinds, T.E. 1974. Development of spruce-fir stands following spruce beetle outbreaks. U.S. Department of Agriculture Forest Service Research Paper RM-131.

Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

Smith, J.H. 1954. A cooperative study of Engelmann spruce-alpine fir silviculture and management. Northwest Science 28:157-165.

Smith, W.K. 1981. Temperature and water relation patterns in subalpine understory plants. Oecologia 48:353-359.

Spurr, S.H. and Barnes, B.V. 1980. Forest Ecology, Third Edition. Wiley, New York.

Stewart, G.H. 1986. Forest development in canopy openings in old-growth Pseudotsuga forests of the western Cascade Range, Oregon. Canadian Journal of Forest Research 16:558-568.

Stewart, G.H. 1988. The influence of canopy cover on understorey development in forests of the western Cascade Range, Oregon, U.S.A. Vegetatio 76:79-88.

Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284-307.

Thompson, J.N. 1977. Patch dynamics in a biennial herb and resource availability to a specialized herbivore. Bulletin of the Ecological Society of America 58:9.

Thompson, J.N. 1978. Within-patch structure and dynamics in Pastinaca sativa and resource availability to a specialized herbivore. Ecology 59:443-448.

Thompson, J.N. 1980. Treefalls and colonization patterns of temperate forest herbs. American Midland Naturalist 104:176-184.

Thornbury, W.D. 1965. Regional Geomorphology of the United States. Wiley, New York.

Vale, T.R. and Parker, A.J. 1980. Biogeography: research opportunities for geographers. Professional Geographer 32:149-157.

Veblen, T.T. 1982. Growth patterns of Chusquea bamboos in the understory of Chilean Nothofagus forests and their influences in forest dynamics. Bulletin of the Torrey Botanical Club 109:474-487.

Veblen, T.T. 1985. Stand dynamics in Chilean Nothofagus forests. Pp. 35-51 in S.T.A.Pickett and P.S. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Veblen, T.T. 1986a. Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. Ecology 67:644- 649.

Veblen, T.T. 1986b. Age and size structure of subalpine forests in the Colorado Front Range. Bulletin of the Torrey Botanical Club 113:225-240.

Veblen, T.T. In Press. Regeneration dynamics. Chapter 4 in Glenn-Lewin, D.C. (ed.), Plant Succession. Chapman-Hall, London.

Veblen, T.T. and Ashton, D.H. 1978. Catastrophic influences on the vegetation of the Valdivian Andes, Chile. Vegetatio 36:149-167.

Veblen, T.T., Ashton, D.H., Schlegel, F.M. and Veblen, A.T. 1977. Distribution and dominance of species in the understorey of a mixed evergreen-deciduous forest in south-central Chile. Journal of Ecology 65:815-830.

Veblen, T.T., and Lorenz, D.C. 1986. Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. Physical Geography 7:1-24.

Veblen, T.T., Hadley, K.S., Reid, M.S., and Rebertus, A.J. 1989a. Blowdown and stand development in a Colorado subalpine forest. Canadian Journal of Forest Research (In Press).

Veblen, T.T., Hadley, K.S., Reid, M.S., and Rebertus, A.J. 1989b. Stand response to spruce beetle outbreak in Colorado subalpine forests. Manuscript in review.

Veblen, T.T., Veblen, A.T., and Schlegel, F.M. 1979. Understory patterns in mixed evergreen-deciduous Nothofagus forests in Chile. Journal of Ecology 67:809-823.

Weber, W.A. 1976. Rocky Mountain Flora. Colorado Associated University Press, Boulder, Colorado.

Weber, W.A. 1987. Colorado Flora: Western Slope. Colorado Associated University Press, Boulder, Colorado.

Whipple, S.A. and Dix, R.L. 1979. Age structure and successional dynamics of a Colorado subalpine forest. American Midland Naturalist 101:142-158.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review 45:229-299.

White, P.S. and Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. Pp. 3-13 in S.T.A.Pickett and P.S. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 26:1-80.

Whittaker, R.H. 1962. Classification of natural communities. Botanical Review 28:1-239.

Whittaker, R.H. 1975. Communities and Ecosystems. 2nd Edition. Macmillan, New York.

Wilson, M.V. 1988. Within-community vegetation structure in the conifer woodlands of the Siskiyou Mountains, Oregon. Vegetatio 78:61-72.

Woods, K.D. and Whittaker, R.H. 1981. Canopy-understory interaction and the internal dynamics of mature hardwood and hemlock-hardwood forests. Pp. 305-323 in West, D.C., Shugart, H.H., and Botkin, D.B. (eds.), Forest Succession: Concepts and Application. Springer-Verlag, New York.

Young, D.R. and Smith, W.K. 1979. Influence of sunflecks on the temperature and water relations of two subalpine understory congeners. Oecologia 43:195-205.

Young, D.R. and Smith, W.K. 1980. Influence of sunlight on photosynthesis, water relations, and leaf structure in the understory species Arnica cordifolia. Ecology 61:1380-1390.

Young, D.R. and Smith, W.K. 1982. Simulation studies of the influence of understory location on transpiration and photosynthesis of Arnica cordifolia on clear days. Ecology 63:1761-1770.

Young, D.R. and Smith, W.K. 1983. Effect of cloudcover on photosynthesis and transpiration in the subalpine understory species Arnica latifolia. Ecology 64:681-687.

Zamora, B.A. 1982. Understory development in forest succession: an example from the inland Northwest. Pp. 63-69 in Means, J.E. (ed.), Forest Succession and Stand Development Research in the Northwest. Forest Research Laboratory, Oregon State University, Corvallis.

Zinke, P.J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43:130-133.